THE RESPONSE OF CULICIDAE TO VISUAL STIMULI

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THE RESPONSE OF CULICIDAE TO VISUAL STIMULI

by

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of the requirements for the degree of
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Abstract

Response of Culicidae to visual stimuli of various colours and shapes was studied in the Tintamirre National Wildlife Area, New Brunswick, in 1977 and 1978. Culicidae were collected from three-dimensional, cube-shaped, funnel target traps of five different colours. The collections indicated a differential preference for the five colours. Aedines and Mansonia perturbans preferred black, red and blue as the most attractive colours, while yellow and white were consistently unattractive. M. perturbans showed substantial colour differentiation in the day and night time collections. The percent luminous reflectance of the light reflected from each colour-stimulus target was inversely proportional to the numbers of Culicidae trapped in the target (i.e. a decrease in the luminous reflectance, the more mosquitoes collected). This trend was fairly consistent throughout 1977 and 1978 but discrepancies did occur.

M. perturbans landed in greater numbers on filters transmitting wavelengths of 480-600 nm and 400-480 nm. A secondary response occurred to 300-400 nm. Low numbers landed on 620 nm and all longer wavelengths.

Four species of Aedes and M. perturbans were shown to respond in greater numbers to cube targets than pyramids while A. punctor was collected in greater numbers from pyramids. While no species were taken exclusively at any of the levels, most mosquitoes were collected in cube and pyramid targets exposed at the 122 and 183 cm levels. Aedines and M. perturbans differentially selected the end or projecting parts of the rectangular (oblong) targets. Few numbers were collected from the center portion.

Recommendations for further studies are discussed as well as suggestions for the application of these findings for personal protection against mosquitoes.

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Introduction

Among the haematophagous Diptera, members of the Culicidae have by far the greatest medical and economic significance, a significance recognised since classical times. Aristotle recognised the role of mosquitoes in the occurrence of relapsing fever, a relationship discussed in the Ebers papyrus (circa 1600 BCE), and known to the contemporary Mesopotamian or Hindu and Chinese cultures of that era (Dampier, 1948). Indeed, the Roman engineer Collumela (150-50 BCE) wrote on the inadvisability of building a house close to a marsh, because the latter "... always throws up noxious and poisonous steams during the heats, and breeds animals armed with mischievous stings, which fly upon us in exceedingly thick numbers, whereby hidden diseases are contracted." (Smith, et al., 1973). However it was not until the time of Ross (1857-1932) that it was realized that Plasmodium vivax, P. falciparum and P. malariae (the causative agents of human malaria) are transmitted by Anopheles. Aedes aegypti[1], among other culicids, has been indicated as a vector of the filariids Wuchereria bancrofti and Brugia malayi, the causative agents of filariasis, a disease of humans found worldwide in the tropics and subtropics; the principal vector of the virus causing yellow fever, a disease of humans, monkeys and rodents, found in the American and African tropics and subtropics and one of the principal vectors of the virus causing dengue, a disease of humans found worldwide in the tropics and subtropics. Other mosquitoes are vectors of several viruses causing encephalitis, a disease of humans and horses, found in the United States, Canada, South America, Europe and Asia. It is still relatively unknown to what extent diseases of wild animals are transmitted by mosquitoes.

[1] See Appendix 1

However they are known to be vectors of avian malaria, some filariids and trypanosomes.

The importance of Culicidae is not always associated with their transmission of diseases. In Canada, relatively little human disease transmission occurs, with the emphasis being on irritation directly from bites or indirectly from possible secondary infections, anemia through loss of blood, allergic responses and psychological trauma at having biting flies about the body.

Transmission of pathogens and harassment by mosquitoes is inevitably associated with their blood-feeding propensities, and this in turn is mediated by their host-seeking behaviour. Insight into such host-seeking behaviour may prove an additional measure for control of mosquito-born pathogens and/or assist in alleviating the annoyance caused by them. Our knowledge of the stimuli which guide mosquitoes in their search of host animals and induce biting and/or feeding is progressively increasing, in part through extension (by analogy) of information gathered on other groups of biting Diptera. However, such analagous information can only be applied in a most general way and detailed studies are required to determine precisely the influence of mechanical, visual, chemical, thermal and hygral stimuli on the host-seeking behaviour of individual species of mosquitoes. It is the objective of this study to provide a more precise evaluation of the influence of mechanical and visual stimuli (particularly colour and shape) on the host-seeking behaviour of some native culicids in their natural environment of the Tantramar Marshes of New Brunswick, Canada.

The response to coloured visual stimuli by Culicidae has been

studied by numerous authors who measured the spectral sensitivities of the eyes using behavioural techniques which varied widely in sophistication. Some of the earlier observations show a preference or an attractance to dark colours rather than light colours by mosquitoes (Howlett, 1910; Eckstein, 1920). Brighenti (1930) working with Anopheles maculipennis counted landings of mosquitoes on coloured ceilings of cattle sheds and concluded the descending order of preference of colours to be red, violet, yellow and white. Smart and Brown (1956) showed a decreased response of adult Aedes mosquitoes to Negroes, Orientals and Caucasians respectively, indicating skin hue to have a differential affect on landing response of Aedes.

Brett (1938) was apparently the first to suggest that this preference for darker colours may be a response to surfaces with a low reflectance factor. His work with A. aegypti showed a preference for black, while light-yellowish khaki and yellow were not landed on in great numbers. He concluded that A. aegypti has colour vision. Brown's (1951, 1954) observations on some Canadian mosquitoes supported Brett (1938) in that attractiveness of certain coloured cloths varied inversely with reflectivity or brightness between wavelengths of 475 and 625 nm. The lower the reflectivity (i.e.black) the more attractive the cloth. O'Gower (1963) found the dominant stimuli affecting A. aegypti, during the appetitive stage, are visual reflectance and appearance. The mosquitoes preferred black moist surfaces to grey moist surfaces. In agreement were Gilbert and Gouck (1957), who compared landing rates on coloured paper disks for A. aegypti, A. taeniorhynchus and A. sollicitans. The disks were treated with dyes of the primary and secondary colours in a range of shades. The

darker shades of each colour attracted the most A. aegypti while the lighter shades attracted most A. taeniorhynchus. The darker shades of the brighter colours (yellow, orange) and the lighter shades of the darker colours (blue) were the most attractive to A. sollicitans.

Sippel and Brown (1953) rendered objects more attractive by an increase in black and white interface in a checkerboard pattern, a principle which Haufe and Burgess (1960) employed in their black and white mosquito traps.

What is in many respects an interesting feature of observations on other insects is that the visible spectrum extends into the near ultraviolet region. Breyev (1963) showed ultraviolet traps were collecting larger numbers of mosquitoes than were the white light traps. The incorporation of such observations into traps for mosquitoes was attempted by Headlee (1937), Weiss (1943) and Williams, et al. (1955), who showed the effectiveness of light traps increased with shorter wavelengths and ultraviolet lamps were shown to take larger numbers of mosquitoes. In an attempt to establish the spectral sensitivity of mosquitoes, and avoiding the use of the word colour, Delong (1954) observed increases in mosquito activity to spectral beams and colour filters within the 364-400 nm range. Fedder and Alekseyev (1965) tried to establish the importance of personal protection from biting flies, including Culicidae, by the use of unattractive coloured clothing. They established black garments to be most attractive for Culicidae when exposed as clothing on people, while white, yellow and green are less attractive.

The shape of an object and its role in the attraction of mosquitoes has not been extensively studied and in fact, no specific reports on

response of mosquitoes to geometric forms were encountered. Studies on mosquitoes preference for targets with protruding surfaces rather than flat ones indicated dimension to be of some importance (Kellogg and Wright, 1962), while Brown (1952) demonstrated the importance of contour in attractiveness by the use of cardboard cubes carrying black and white in equal amount in a checkerboard or striped pattern.

Laarman (1955, 1958) in laboratory studies of anopheline mosquitoes, indicated that host-seeking consists of a special type of behaviour pattern in which both internal and external stimuli play specific parts. He considered that several factors acting as external stimuli affect the orientation to a host by the mosquitoes. He divided these factors into:

(a) visual cues - size, shape, movement, contrasting action, reflection of light.

(b) physical cues - radiation and convective heat, moisture, sound, surface structure.

(c) chemical cues - CO_2 and other factors - generally considered as odours.

Laarman (1955) suggested, by referring to observations on the behavioural mechanism of other animals (Tinbergen, 1942; Dethier, 1947), that in addition the insects' need for a blood meal leads to an appetitive behaviour which induces the insect to follow a chain of behavioural responses, each being released by a particular stimulus. At the end of this chain of reactions, if undisturbed, the insect will have satisfied its appetite. Bradbury (1972) summarizes the division by Smith (1966) and further sub-division by Golini (1970) of the series of stages involved in the feeding of Simuliidae as follows:

Phase I Appetitive Behaviour

Stage 1 Habitat Selection

2 Upwind Orientation

3 Near Orientation

4 Landing Behaviour

5 Crawling and Burrowing

Phase II Consummatory Reaction

6 Probing and Feeding

Phase III Cessation of Feeding

Phase IV Physiological State of Rest

This generalized scheme can be applied to the feeding behaviour of mosquitoes, with some minor modifications. An obvious modification would be in eliminating Stage 5 since mosquitoes, if they land on an inappropriate feeding area, will usually take off and land again on a different area rather than crawl around.

Briefly the hierarchy of the host-seeking behaviour is as follows: Stage 1 is believed operative, as species of biting flies are known to prefer particular habitats (Davies and Peterson, 1957; Bennett, 1960). Biting flies in the physiological state searching for a blood meal will do so in their preferred habitat.

Stage 2 involves olfactory cues such as CO_2 and other host emanations which function to orient the fly to the host (Hocking, 1971). Smith (1966) proposed that the chance of a fly orienting upwind directly to an odour cloud or CO_2 is slight and that vision too is involved, but only in as much as it is involved in navigation. The distance whereby visual stimulation due to the shape, colour, size and movement of the host actually direct the fly to the host is considered to be

near orientation (Stage 3).

Stage 4 is effective only when the insect has located the host, Stage 5 when it has landed and Stage 6 when bloodfeeding is initiated. Phases III and IV result in a relative state of rest, after the fly has engorged and the digestion of the blood meal proceeds.

Man is aware of environmental situations through sensory perceptions which he can subsequently verbalize. Mosquito perception of its environment can only be interpreted by observing the insects' behavioural responses. The response to the visual stimuli of shape and colour as it applies to the host-seeking process by mosquitoes in the near orientation stage of Phase I (Appetitive) behaviour is the primary concern of this study. Specifically, the study was designed to explore the response of mosquitoes to three-dimensional targets of different shapes and spectral compositions exposed at various heights, under natural conditions, and to transmitted wavelengths, of the electromagnetic spectrum under laboratory conditions.

Materials and Methods

The studies were conducted in the Tintamirre National Wildlife Area, New Brunswick, situated approximately 11 km northeast of the town of Sackville, New Brunswick, Canada (Fig. 1). The area supports a variety of habitats, as well as a diversity of breeding mosquitoes. Such an area provided the opportunity to study the responses of numerous species of mosquitoes to visual stimuli. The area has been thoroughly described by Herman and Bennett (1976) and Meyer and Bennett (1976).

Collections were made in two sites - the Sylvan Site #1 and Lacustrine Site #2 (Fig. 1). The dominant vegetation of Site #1 is black spruce, Picea mariana, with a maximum canopy height of approximately 15 m. Mosses are the major vegetation of the forest floor. The predominant vegetation of the lacustrine habitat, Site #2, includes cattail (Typha spp.) and sedges (Carex spp.), burreed (Sparganium spp.) and sweet flag (Acorus spp.). This study site is located close to the lake shore in an alder fringe. Alnus spp., with a canopy height of approximately 3 m, is the dominant vegetation of the lake shore. The ground cover is comprised of various grasses and shrubs. Studies were conducted in both sites from June to August in 1977 and from May to July in 1978.

The responses of mosquitoes to visual stimuli were studied as follows:

1. Response of mosquitoes to variously coloured three-dimensional square targets.

2. Response of mosquitoes to three-dimensional targets of two geometrical shapes and exposed at four strata.

Fig. 1 Aerial View of the Tintamirre National Wildlife Area, New Brunswick. 1. Sylvan Site

2. Lacustrine Site

A. Canadian Wildlife Service Field Station


Large
Lake
N
1
2
Long
Lake
A
Front
Lake

3. Response of mosquitoes to regions of three-dimensional black and white rectangular targets.

4. Response of mosquitoes to transmitted light of known wavelength.

Response in Studies 1, 2 and 3 is recorded as the total number of mosquitoes trapped in each three-dimensional target. Response in Study 4 is the total number of mosquito landings on each filter transmitting light of known wavelength.

Temperature was recorded before and after each test in Studies 1, 2 and 3. Observations in the area show that the activity of mosquitoes is greatly reduced at temperatures below 11°C (pers. obs.; Lewis, 1976). If during a test the temperature dropped below 11°C, the trial was repeated at another time.

It is a well documented fact that CO_2 increases the catch per trap for mosquitoes (Newhouse, et al., 1966). During the exposure of targets (traps), CO_2 compressed gas was released from steel cylinders at an approximate rate of 250 cc/min. The emission jet was placed approximately 7 m upwind from the test site (cf. Bradbury and Bennett, 1974).

Target traps were returned to the field laboratory where collected mosquitoes were removed with aspirators. They were then placed in ice-cream boxes, chilled in a refrigerater, and subsequently stored in 70% ethanol for later identification. Mosquito identification was according to Carpenter and LaCasse (1955) and Lewis (1976).

Study 1 Coloured Artboard Study

This study was carried out at Sites #1 and #2 from June to August 1977, and from May to July in 1978, in an attempt to record the response of mosquitoes to different coloured artboards. Collections were made at both sites in anticipation of increased numbers of

mosquitoes. The 1977 collections which were initiated in June, missed a large portion of the Aedes, which are prevalent in May and June in this part of New Brunswick. Therefore to obtain a greater sample of Aedes, the study was repeated in 1978, beginning collections earlier in May. When the numbers of Mansonia collected were proportionally larger than Aedes (increased to approximately 50% of the sample in mid-July 1978), this study was terminated.

In 1977 collections were made at day and at night to see if the response of mosquitoes to coloured stimuli differed at these times. If colour-blind species exist, they are more likely to be found among the nocturnal species. The question is whether the colour vision apparatus has adapted to functioning by night or are the nocturnal species without this ability. In 1978 this study was not repeated, as the 1977 results did not indicate significant differences in the day and night time responses to the coloured targets.

Five, three-dimensional, coloured square targets (black, blue, red, yellow and white) were constructed from Peterborough Artboard[2] (Fig. 2). The artboard was the same as was used by Bradbury and Bennett (1974). Spectral analyses of the coloured board are in Table 1. Table 2 gives the recorded intensity of reflected light from the artboard as measured with a spectroradiometer.

Square frames for the targets were constructed from 25.4 cm X 25.4 cm spruce and assembled into cubes, each side measuring 254 cm^2. Five sides of each cube were covered in the coloured artboard and each of the five sides had a plastic funnel (diameter dimensions: inlet 12.7 cm, outlet 38.1 cm) positioned in the center to provide entry for the mosquitoes to the interior of the cube. The 6th side was outfitted

[2] Peterborough Artboard; Card and Paper Works Ltd.

Fig. 2 Three-Dimensional, Coloured Artboard Targets Suspended 122 cm from Ground Level at the Test Site (Study 1)

Table 1. Tabulated Munsell Reflectance Values for Peterborough Artboard (from Bradbury, 1972)

Peterborough Stimulus Cards	'Derived' Munsell Notation	Luminous Reflectance/ Munsell Value in % Relative to MgO **	Peak Wavelength Millimicrons
No. 1900 Dull Coat White	N9.15/	81.95	
No. 1911 Dull Coat Canary Yellow	7.5Y8.6/ 10.5	70.37	560
No. 1967 Dull Coat Expo Red	7R4.6/ 15	16.37	(580) -700
No. 1968 Dull Coat Expo Blue	6PB3.7/ 14	10.13	450
No. 1909 Dull Coat Black	N1.75/	2.53	

** Luminous reflectance for light source "C", equivalent to average north daylight having a colour temperature of approximately 6,750 degrees Kelvin.

The Munsell System is based on spacing the colours for their appearance under C.I.E. Source, equivalent to a colour temperature of 6,750 degrees Kelvin, which is equal to average North Daylight from a partially overcast sky.

Table 2. Intensity of the Peterborough Artboard at Selected Wavelengths, as Recorded with a Spectroradiometer

Wavelength (nm)	Artboard Colour				
	Black No. 1909	Blue 1968	Red 1967	Yellow 1911	White 1900
380	.261**	.261	.261	.261	.261
400	.065	.065	.065	.065	.065
450	.068	.120	.086	.103	.120
500	.880	.126	.010	.130	.160
550	.229	.284	.076	.421	.340
600	.235	.280	.360	.476	.443
650	.113	.098	.170	.186	.130
700	.019	.029	.044	.044	.030
750	.015	.015	.230	.023	.015

** The values for intensity are microwatts per square centimeter per millimicron.

These values of spectral intensity have been corrected as described in the operation manual for the Model Spectroradiometer SR, Series #140-003. These corrected values may be plotted against wavelength. The area under the curve over any particular wavelength interval is equal to the amount of radiant energy intensity in the wavelength interval.

with a mesh sleeve to provide access to the interior of the cube to clear the contents. The trapping in the targets is a result of a peculiarity in the mosquitoes' searching pattern that allows them to seek entrance into the funnels. This type of trap did not prove useful for trapping other biting dipterans (Simuliidae and Tabanidae), as they did not show this tendency to seek entrance to the interior of the traps by way of the funnels.

Before constructing the three-dimensional square targets with the funnel traps, two-dimensional sticky traps as described by Bradbury and Bennett (1974) were used in this study. This sticky trap method was unsuccessful in trapping Culicidae. Observations show that mosquitoes were able to avoid being trapped on the sticky surface due to their long legs which provided enough leverage for the mosquitoes to hover and thus pull their legs free.

Clothes line wire was strung between two trees at Site #1 and between two poles, positioned by the researcher, at Site #2. The five targets were suspended by twine, approximately 122 cm from the ground (Fig. 2).

Each test period involved a new order of arrangement of colours according to a table of random numbers. Due to limited CO_2 source, 4 h was the maximum allowable time of exposure of the targets for one trial. The day and night time exposures were usually between 0800-1300 h, and 2000-2400 h respectively.

Study 2 Shape Preference Study

The intent was to record the responses of mosquitoes to geometrical shape. The study involved two, three-dimensional cubes and two pyramids, with one shape being black and the other white. Colour was

incorporated into the design to evaluate the importance of colour in the mosquitoes choice of target. Each target had the same funnel entry and mesh sleeve as described in Study 1. The sleeves of the pyramids were positioned at the top point of the pyramid, under a removable point. The dimensions of the targets and the funnels in this case are slightly larger than in Study 1. The dimensions in this case are as follows: Cube: each side 406 cm^2; Pyramid: length 406 cm, width 406 cm, height 352 cm; Diameter of Funnels: inlet 50.8 cm, outlet 38.1 cm.

The exposure time and apparatus was the same as that described for Study 1. However as stratification of mosquitoes is well documented (Haddow, et al., 1947) the targets were exposed at alternating heights of 61 cm, 122 cm, 183 cm and 244 cm (Fig. 3) to collect possible stratified species. The series of exposures are given in Table 3.

Study 3 Discrimination of Regions of Rectangular Targets

Some authors have indicated that biting flies orient to different regions of inanimate objects (Wenk and Schlörer, 1963) and Study 3 was undertaken to determine which area of an oblong or rectangular shaped target mosquitoes would orient. Two, three-dimensional, rectangular targets, one black and one white, were constructed so that the interior was partitioned into three compartments (two end and one center). Each compartment was equipped with funnel entries (Fig.4a). Thus the bottom and two sides of each compartment had funnels and the top had the mesh sleeve as described previously.

The exposure apparatus (Fig.4b) and time were the same as was described for Studies 1 and 2.

Study 4 Kodak Filter Experiment

Fig. 3 Cubes and Pyramids Exposed at Varying Strata (Study 2)

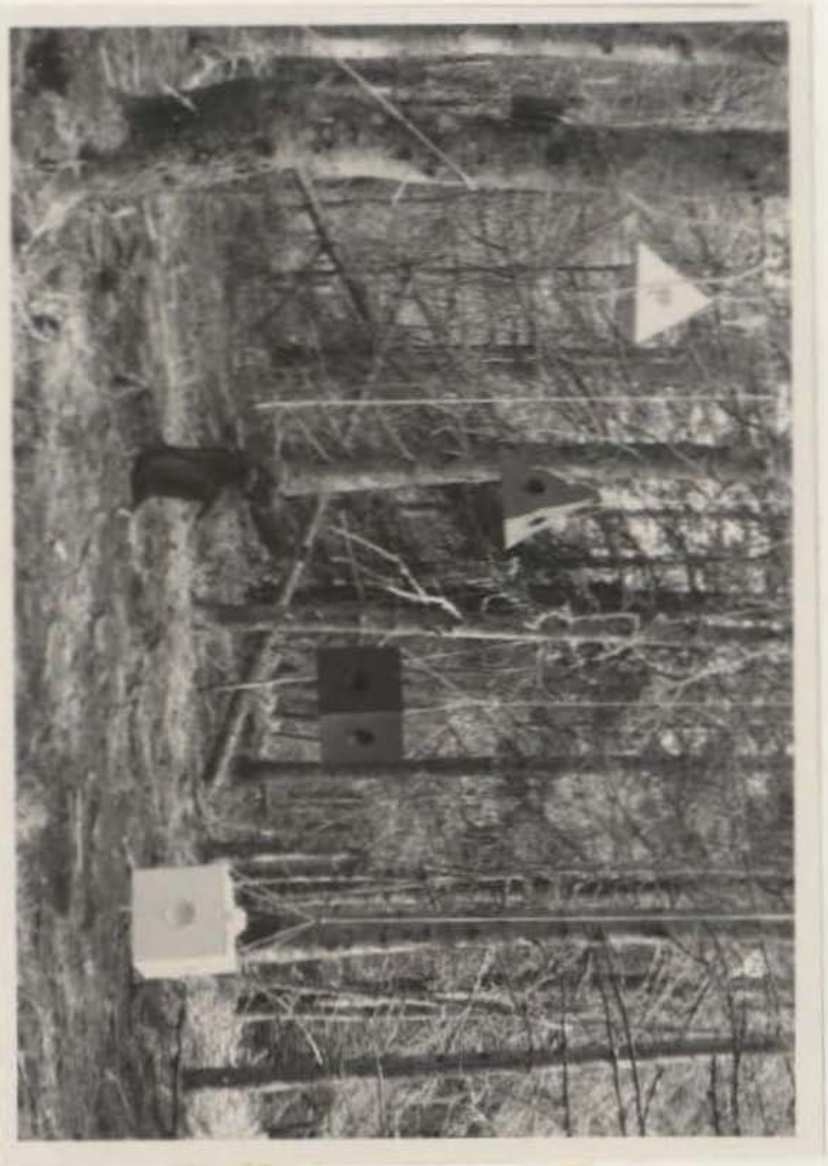


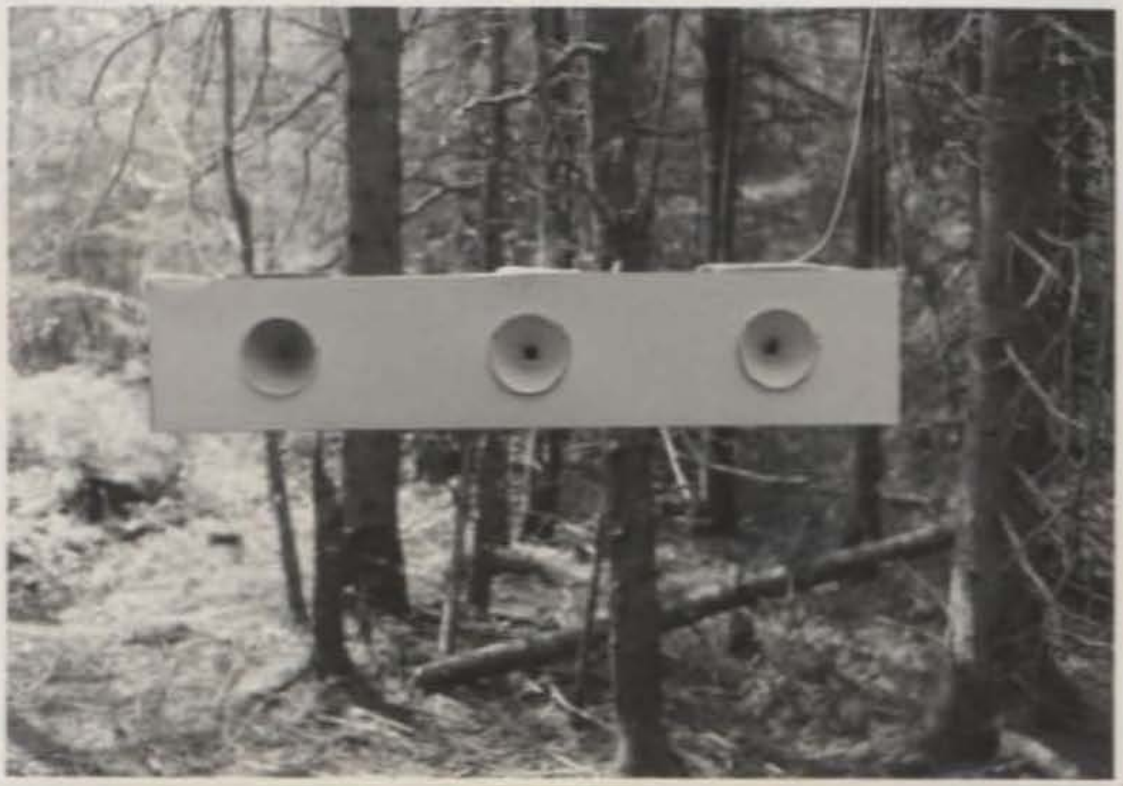
Table 3. Exposure Format for the Targets of the Preferred Shape Study (Study 2)

Target	Height of Exposed Target (cm) Trial 1*	Trial 2	Trial 3	Trial 4
Black square	61	122	183	244
Black triangle	122	183	244	61
White square	183	244	61	122
White triangle	244	61	122	183

*Each trial was repeated four times.

Fig. 4a Close-up of Funnel on Rectangular Targets of Study 3

b Exposure Arrangement of Rectangular Targets



This was designed to record the response of mosquitoes to transmitted light of known wavelength as opposed to Studies 1, 2 and 3 in which the responses recorded were to reflected light from the coloured artboard. This study was performed in the confines of the Canadian Wildlife Service Field Station (Fig. 1A).

Five Kodak filters, which transmit narrow bands of wavelengths of light, were selected to represent the electromagnetic spectrum from 300 nm (ultraviolet region) to 700 nm (infrared region). The transmittance data for the five filters are given (Table 4). Further technical information can be found in Kodak publication B3. Table 5 gives the intensity of the filters at selected wavelengths, as recorded with a spectroradiometer.

This experiment was divided into two parts. As each of the three filters tested transmit near infrared in addition to the wavelengths given in Table 4, part A was devised to test whether the transmitted infrared was causing a differential response in landings on the filters. It involved the recording of mosquito landings on two filters exposed at the same time. Paired 47B, 61, and 92 filters were exposed simultaneously with one of the pair in series with an infrared cut-off filter. Three, ten min recordings of landings were made for each of the pairs of filters. The series of exposures are in Table 6. Ultraviolet and infrared were not tested in this manner as ultraviolet does not transmit infrared and infrared paired with an infrared cut-off filter gives a transmittance of zero. Kodak filters obey the Bouguer-Lambert Law which states that the spectral transmittance of two or more filters used simultaneously is equal to the product of the spectral transmittance of each filter, thus filters can be paired without

Table 4. Spectral Transmittance Data for the Kodak Filters

Kodak Filter No.	% Luminous Transmittance	Name or Visible Colour	Transmittance (nm)	Dominant Wavelength
301A		Infrared Cut-off (IRCO)	80% of visible light up to 640	
18A		Ultraviolet	300-400	
47B	0.79	Blue	400-500	452.7
61	16.8	Green	480-600	533.8
92	2.6	Red	620-700	646.2
88A		Infrared	720-	

Table 5. Intensity of Each Filter at Selected Wavelengths, as recorded with a Spectroradiometer

Wavelength (nm)	Filter No. 18A	47B	61	92	88A
380	.261**	.261	.261	.261	.261
400	.039	.489	.065	.261	.065
450	.007	.753	.086	.009	.009
500	.005	.025	8.530	.006	.631
550	.009	.005	19.300	.005	.005
600	.008	.004	.110	.017	.004
650	.009	.004	.004	4.340	.004
700	.026	.004	.004	2.850	.004
750	.091	.106	.122	.866	.004

** The intensity values are in microwatts per square centimeter per millimicron

These values of spectral intensity have been corrected as described in the operation manual for the SR-Model Spectroradiometer, Series #140-003. These corrected values may be plotted against wavelength. The area under the curve over any particular wavelength interval is equal to the amount of radiant energy intensity in the wavelength interval.

Table 6. Format of Exposure of Paired Experiments of Filters of Study 4, Part A

Filter	47B + IRCO*	61 + IRCO	92 + IRCO
47B	+**	-	-
61	-	+	-
92	-	-	+

*IRCO - Infrared cut-off filter

**Each + constitutes one test, and each test was repeated three times.

changing the transmittance pattern of the filters.

Each filter was tested against all others in part B, again giving the mosquitoes a two filter choice. The format of exposure of the filters is in Table 7. The filters were exposed to the mosquitoes for three, ten min trials, during which landings were recorded using a hand counter.

The apparatus for display of the filters was designed and constructed as follows. It is in two sections (Fig. 5). The front box section was constructed of plywood, and was square in shape (dimensions-length 508 cm, width 406.4 cm). The front end of the box was a sliding plexiglass window which enabled the viewer to count the landings on the filters which were mounted at the opposite end of the box. This end was removable and had two square windows cut slightly smaller than the filters which measured 76.2 cm X 76.2 cm (Fig. 6). Cardboard frames were placed on the filters for easy handling. The filters were positioned in slots and taped with black tape to hold them tightly over the edges of the windows to prevent light leakage. The mosquitoes were placed inside this box, the interior of which was painted a flat black.

The rear section of the apparatus was rectangular in shape and housed the tungsten bulb light source. The box was made of square wood frames and was sealed on five sides with sheets of artboard stapled to the frames. The box was open at one end and built slightly larger than the front section so that the rear section slid over the front box with a 25.4 cm overlap. A General Electric tungsten floodlamp (100 watts) recommended by Kodak was situated at the rear of this box and provided the illumination for the filters positioned over the

Table 7. Format of Exposure of Paired Experiments of Filters of Study 4, Part B

Filter	Colour	18A	47B	61	92	88A
18A	Ultraviolet	-	-	-	-	-
47B	Blue	+*	-	-	-	-
61	Green	+	+	-	-	-
92	Red	+	+	+	-	-
88A	Infrared	+	+	+	+	-

*Each + constitutes one test and each test was repeated three times.

Fig. 5 Apparatus for Display of Kodak Filters (Study 4)

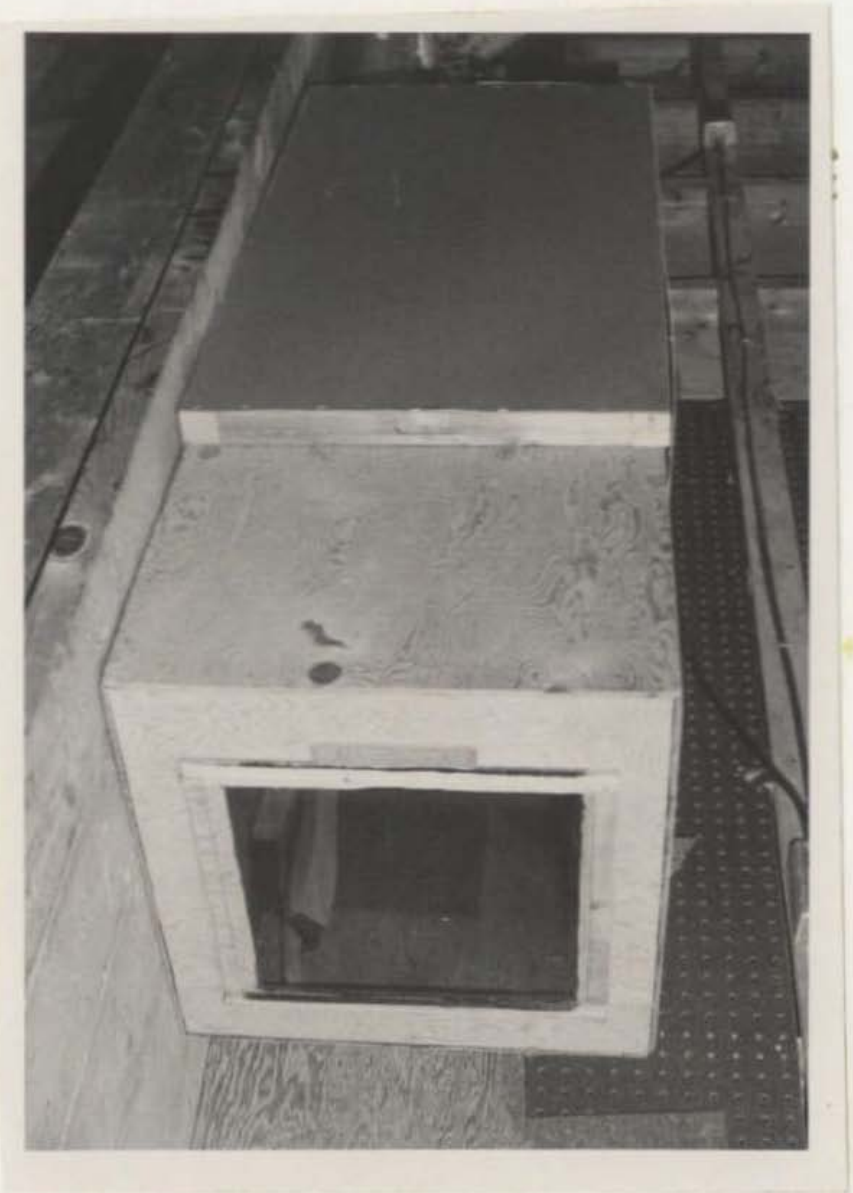
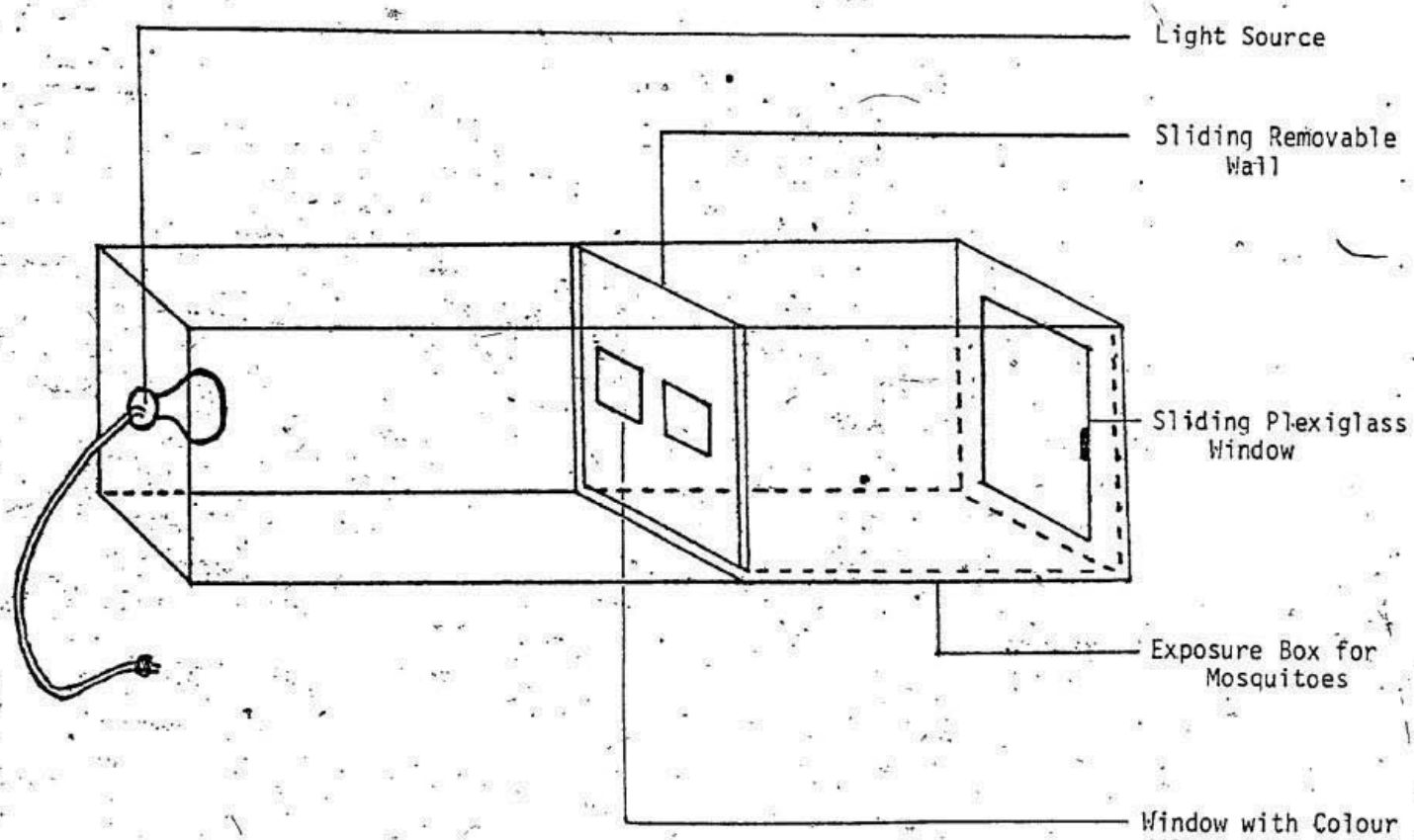


Fig. 6 Diagram of Apparatus for Display of Kodak Filters Showing Interior Design


Light Source
Sliding Removable Wall
Sliding Plexiglass Window
Exposure Box for Mosquitoes
Window with Colour Filter

windows on the rear of the front box section (Fig. 6). The experiment was carried out in total darkness with illumination being light from the tungsten light source transmitted through the filters.

One hundred Mansonia perturbans were collected around livestock with aspirators and placed, in total darkness, inside the exposure box. The light source was switched on and landings on each filter were recorded for a ten min period. This trial was repeated three times for each paired filter tested. Between each trial the light was turned off and the mosquitoes were left in darkness for about five min. During this time the mosquitoes ceased flying and rested on the sides and bottom of the box.

In North America, Mansonia perturbans is sometimes considered to be of the genus Coquillettidia. However, in this thesis Mansonia perturbans is used, according to Carpenter and LaCasse (1955).

Results

Study 1 Coloured Artboard Study

Two sites were used to record responses of mosquitoes to five coloured targets (Table 8). Some differences in the species and numbers of mosquitoes that were collected at the sylvan and lacustrine sites were noted.

In 1977, a total of 223 aedines (13.7% of total mosquitoes) were collected, whereas in 1978, 512 aedines (58.7%) were collected (Table 8). Aedines, in the Tantramar Marshes, appear in their greatest numbers early in May (Lewis 1976). In 1977, field studies did not begin until June and hence in this year, the proportion of aedines collected was lower than in 1978. Conversely, in 1977, 86.1% of the mosquitoes collected were M. perturbans, while in 1978, this species only represented 41.3% of the total mosquitoes. M. perturbans is a late summer form, appearing in July and persisting through August (Lewis 1976). In 1978, field testing was terminated in July. This resulted in the major drop in proportion of M. perturbans collected in this year. The same factors contributed to a lowered total mosquito collection in 1978. In 1977, aedine mosquitoes represented 12.7% of the mosquitoes collected at Site #1, and 14.3% of those at Site #2; in 1978, aedines represented 49.9% and 75.7% of the mosquitoes in Sites #1 and #2 respectively. There was no indication that either site was particularly favoured by either aedines or M. perturbans.

It is evident from the data (Tables 9, 10; Figs. 7, 8) that there was a differential response to the various coloured boxes among the mosquitoes. Throughout the 1977 and 1978 study, only three species, A. cantator, A. punctor and M. perturbans were collected in sufficient

Table 8. Species of Culicidae Collected from Three-Dimensional, Coloured Artboard Targets at Each Site (Study 1)

Species	1977* Site 1	1977* Site 2	1977* Total	1978* Site 1	1978* Site 2	1978* Total	Grand Total
Aedes abserratus	1	1	2	4	0	4	6
A. canadensis	1	0	1	9	4	13	14
A. cantator	41	125	166	135	130	265	431
A. cinerius	2	2	4	3	1	4	8
A. excrucians	4	3	7	11	4	15	22
A. punctor	16	20	36	97	79	176	212
A. stimulans	1	3	4	0	1	1	5
A. vexans	0	3	3	28	6	34	37
Anopheles walkeri	0	1	1	0	0	0	1
Culiseta morsitans	0	1	1	0	0	0	1
Mansonia perturbans	455	940	1395	288	72	360	1751
	521	1099	1620	575	297	872	2492

* 1977 collections June through August
1978 collections May through July

Table 9. Species of Culicidae Collected from Three-Dimensional, Coloured Artboard Targets, 1977 (Study 1)

Species	Black		Red		Blue		White		Yellow		Total
Aedes abserratus	0		0		0		2		0		2
A. canadensis	0		1		0		0		0		1
A. cantator	46	28%	37	22%	67	40%	10	6%	6	4%	166
A. cinerius	2		0		1		1		0		4
A. excrucians	2		2		2		1		0		7
A. punctor	15	42%	9	25%	3	8%	2	6%	7	19%	36
A. stimulans	2		1		1		0		0		4
A. vexans	0		0		3		0		0		3
Anopheles walkeri	0		0		1		0		0		1
Culiseta morsitans	1		0		0		0		0		1
Mansonia perturbans	627	45%	346	25%	179	13%	161	12%	82	6%	1395
	695		396		257		177		95		1620

Table 10. Species of Culicidae Collected from Three-Dimensional, Coloured Artboard Targets, 1978 (Study 1)

Species	Black	Red	Blue	White	Yellow	Total
Aedes abserratus	4	0	0	0	0	4
A. canadensis	5	2	3	3	0	13
A. cantator	117 44%	45 17%	81 31%	5 2%	17 6%	265
A. cinerius	0	0	4	0	0	4
A. excrucians	1	0	14	0	0	15
A. punctor	66 37%	48 27%	47 27%	8 5%	7 4%	176
A. stimulans	1	0	0	0	0	1
A. vexans	16	4	11	2	1	34
Mansonia perturbans	147 41%	39 11%	149 41%	18 5%	7 2%	360
	357	138	309	36	32	872

Fig. 7 Landing Responses of Culicidae to Three-Dimensional, Coloured Artboard Targets, 1977 (Study 1)

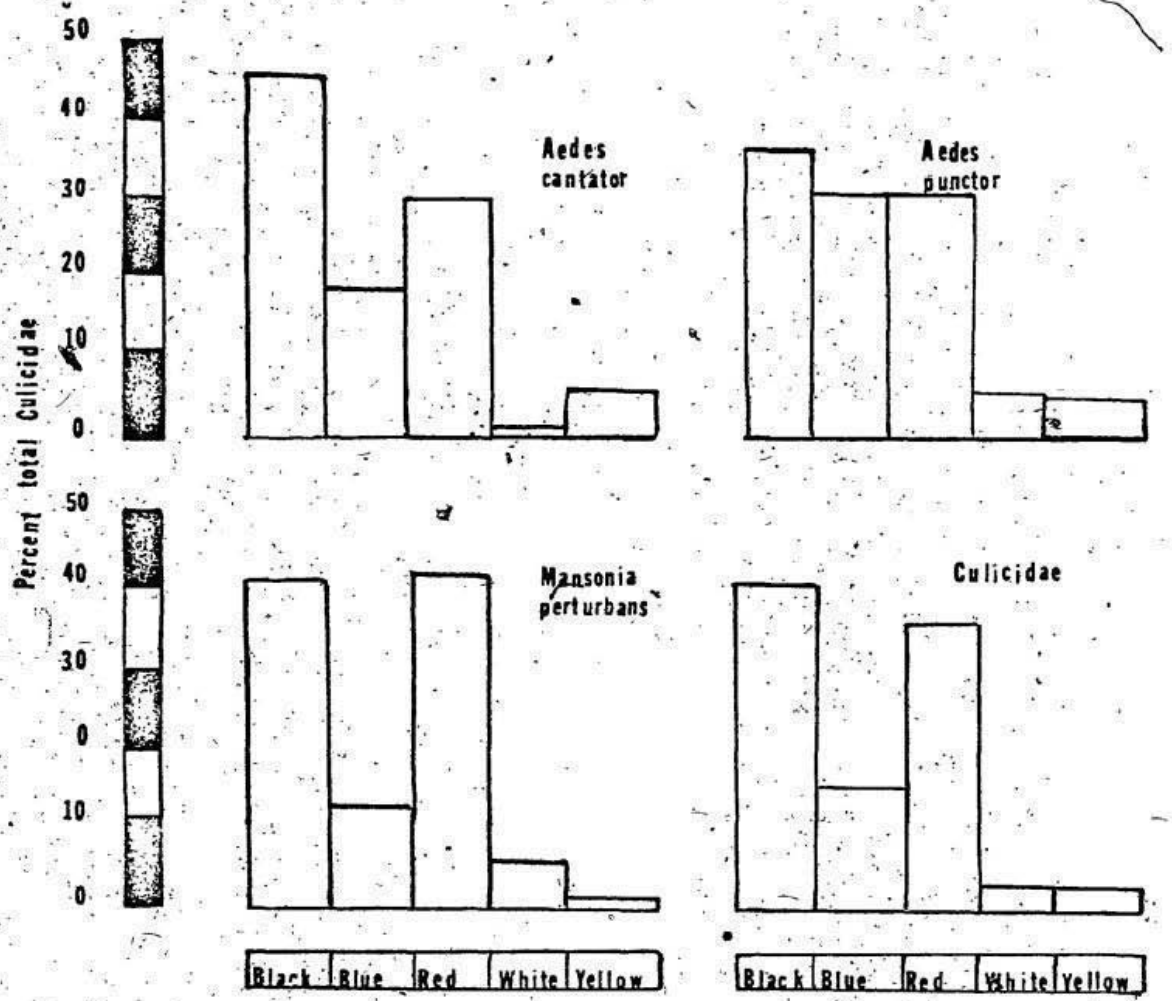
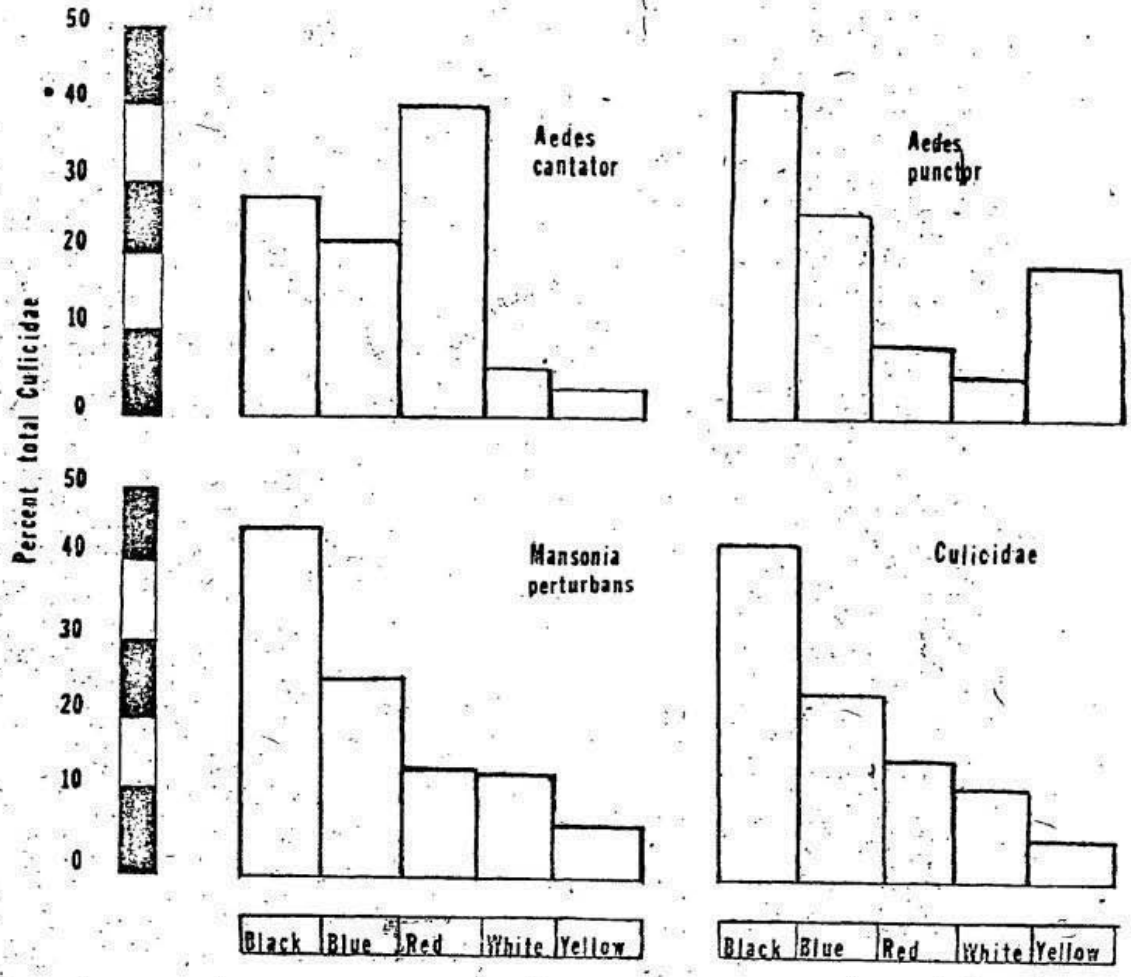

Percent total Culicidae
50
40
30
20
10
0
Aedes cantator
Aedes punctor
Mansonia perturbans
Culicidae
Black
Blue
Red
White
Yellow

Fig. 8 Landing Responses of Culicidae to Three-Dimensional, Coloured Artboard Targets, 1978 (Study 1)


Percent total Culicidae
50
40
30
20
10
0
Aedes cantator
Aedes punctor
Mansonia perturbans
Culicidae
Black
Blue
Red
White
Yellow

numbers to merit discussion. Overall Culicidae totals show black to be the most attractive colour target in 1977 followed by red, blue, white and yellow (Fig. 7). In 1978 similar results show black to be the most attractive followed by blue, red, white and yellow (Fig. 8).

A. punctor was taken more frequently from black and red targets than from the other three. The 1977 A. punctor collections were numerically low, thus a real indication of colour preference is difficult to deduce from the target totals (Table 9). The 1978 results, being somewhat higher and more reliable, show black to be the most attractive target. Blue and red collected equal numbers of mosquitoes and the white and yellow targets were unattractive (Table 10; Fig. 8).

A. cantator was consistent with A. punctor in the apparent unattractiveness of the yellow and white targets in 1977 and 1978. The attraction of the black targets was again seen in the 1978 results for this species, as the targets collected 44% of the species. Blue targets collected 31% and red 17% in this year (Table 10; Fig. 8). Contrary to this in 1977 this species was taken more frequently from the blue targets with 40% from blue, 28% from black and 22% from red targets. It appears that an overall preference for black, blue and red existed but black and blue fluctuated in the first and second most preferred colour positions (Table 9; Fig. 7). If the two years observations for A. punctor are totalled the order of preference of colours was black, red, blue, yellow and white.

M. perturbans results indicated a trend of preference for black, blue and red, while yellow and white colours were unattractive. In 1977, the three most attractive colours, in order of preference were black (43% of the total captures), red (24%) and blue which collected 16% (Table 9; Fig. 7). In 1978, however, blue collected the most mosquitoes

but black and blue were of approximately equal attractiveness, with 41% catch for each colour. Red collected just 11% in 1978 (Table 10; Fig. 8). A Friedman Two-Way Analysis of Variance supports the fact that the differences observed in the numbers of mosquitoes collected from the various coloured traps are significant (in 1977 $p<.001$, in 1978 $p<.001$). Thus the mosquitoes are responding differentially to the colours.

Percent luminous reflectance of the various colours plotted against the numbers of Culicidae collected each year in the boxes, shows that in 1978 the percentage of luminous reflectance of each colour stimulus card was inversely proportional to the numbers of Culicidae coming to and being trapped in the coloured target, that is, a decrease in the luminous reflectance or the coloured target reflecting the least amount of light increases the mosquito catch or increases the attraction. This trend was fairly consistent in 1978 (Fig. 9) except that more mosquitoes were collected from white targets than from yellow targets, even though white had a higher luminous reflectance (Table 1). In 1977, the trend was not as noticeable. More mosquitoes landed on white than on yellow and red collected more mosquitoes than blue even though blue had a lower luminous reflectance. These results indicate that luminous reflectance of an object has an influence on the response of mosquitoes to objects, however the discrepancies observed, especially obvious in the 1977 data, indicated that other factors were influencing the mosquitoes' response to the coloured targets.

If the ranks of the coloured scores are compared by site, black and red occupied the most attractive positions at the sylvan and the lacustrine sites in 1977 and 1978 (Table 11). Yellow and white were consistently unattractive and blue fluctuated at intermediate levels of attractiveness. Thus, in addition to the observations between species and

Fig. 9 Landing Response of Culicidae to Coloured, Three-Dimensional Artboard Targets, as a Function of Luminous Reflectance, 1977 and 1978 (Study 1)

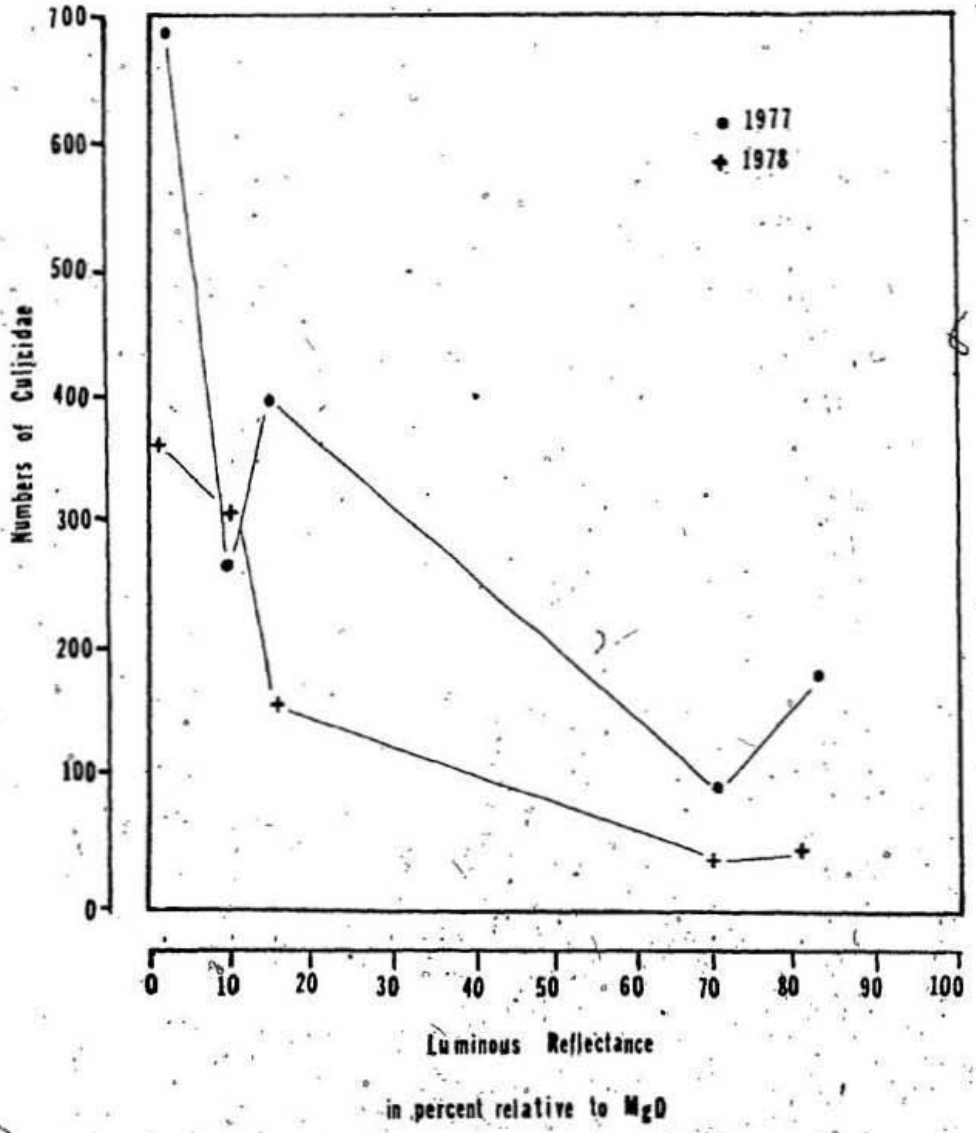

700
600
500
400
300
200
100
0
Numbers of Culicidae
• 1977
+ 1978
0
10
20
30
40
50
60
70
80
90
100
Luminous Reflectance
in percent relative to MgO

Table 11. Numbers of Culicidae Collected in the Coloured Artboard Targets, at the Two Sites in 1977 and 1978 (Study 1)

Colour	1977 Site 1	R*	2	R	Total	1978 Site 1	R	2	R	Total	Grand Total
Black	135	1	560	1	695	236	1	121	1	357	1052
Blue	51	4	206	3	257	92	3	46	3	138	395
Red	105	2	291	2	396	219	2	90	2	309	705
White	40	5	55	5	95	15	4	21	4	36	141
Yellow	52	3	125	4	177	13	5	19	5	32	209
	383		1237		1620	575		297		872	2492

*Rank from Kendall Rank Correlation

years, the Culicidae appeared to be responding to the same coloured artboard at the two sites.

Response of Culicidae to Coloured Artboard at Day and Night

In attempting to determine if there is a difference in response to colour between day and night, it was realized that the only species that could be considered in this respect was M. perturbans, a crepuscular mosquito (Table 12). This mosquito was collected in sufficient numbers at day and at night to provide comparison. The mosquito is an opportunistic feeder and responded to the CO_2 source during the day when it would normally be resting in the vegetation.

During the day, black was the obvious preferred choice with 57% of the numbers caught being from the black targets (Table 13). Blue and red were preferred over yellow and white but when compared to black were relatively unattractive.

At night, Mansonia appeared not to be able to distinguish black and red targets as readily when compared with the day time results. Blue, yellow and white were unattractive as during the day but white caught 12% more mosquitoes at night. Mansonia appeared to be able to distinguish certain colours at night, as it had basically the same preference of colours at night as during the day.

Study 2 Shape Preference Study

As part of the studies on host-seeking behaviour, collections of mosquitoes were made from targets of two geometrical shapes to determine if mosquitoes respond differentially to the geometry of an object. Colour was incorporated into the experiment by having a black and a white target of each shape, to further assess colour preference. Collections were made at four elevations from 61 cm to 244 cm in an effort to cover

Table 12. Species Collected from the Coloured Artboard Targets at Day and Night (Study 1).

Species	Day (0800-1300 h)	Night (2000-2400 h)	Total
Aedes abserratus	1	1	2
A. canadensis	1	0	1
A. cantator	158	8	166
A. cinerius	2	2	4
A. excrucians	5	2	7
A. punctor	30	6	36
A. stimulans	3	1	4
A. vexans	3	0	3
Anopheles walkeri	0	1	0
Culiseta morsitans	0	1	0
Mansonia perturbans	645	750	1395
	848	772	1620

Table 13. Number of Mansonia perturbans Collected from each Coloured Artboard Target, at Day and at Night (Study 1)

Colour	Day	%	Night	%	Total
Black	369	57	257	34	626
Blue	100	16	79	11	179
Red	115	18	232	31	347
White	33	5	128	17	161
Yellow	28	4	54	7	82
	645		750		1395

the natural stratification of the mosquito species. The question arose after Study 1 that perhaps the elevation at which the coloured targets were being exposed was selecting certain species from the mosquito population. Eight species of mosquitoes were collected from the targets but only three of these were in sufficient numbers to merit discussion. The Culicidae totals collected from the two shapes indicate that the square target was twice as attractive as the pyramid (Table 14). The square collected 898, and the pyramid 494. Species observations show M. perturbans and A. cantator to respond preferentially to shapes. Chi-squared analysis of the shape totals results in $p<.01$ for each species, thus the differences observed are significant and these species are selecting squares over pyramids.

A. punctor, on the other hand was taken more frequently from pyramid targets. The $p<.01$ from chi-squared analysis of the A. punctor scores, indicates significant differential response to the pyramid.

The response of the mosquitoes to the black and white targets supported the results of Study 1 in the mosquitoes choice or preference for the black colour over the white colour. A total of 1184 mosquitoes were taken from the black targets and 208 from the white. The black pyramid collected approximately four times the numbers as white pyramids and the black square eight times the numbers as white squares (Table 15). A chi-squared test results in $p<.01$ thus the differences observed in the colour totals are significant.

Specimens of A. cantator were taken at all levels but were most abundant at or about 122 cm from ground level. Fifty-one percent of the mosquitoes were collected from this level and 28% from 183 cm. The 61 cm level and 244 cm level targets did not collect many mosquitoes of this

Table 14. Total Number of Culicidae Captured in Traps of Two Geometrical Shapes Exposed Four Strata (Study 2)

Species	Square	Pyramid	Total	Height (cm) 61	122	183	241	Total
Aedes canadensis	4	2	6	2	1	3	0	6
A. cantator	105	73	178	14	90	49	25	178
A. excitans	0	4	4	0	3	1	0	4
A. punctor	58	78	137	28	51	42	16	137
A. vexans	13	6	19	1	7	11	0	19
Anopheles walkeri	0	3	3	0	0	0	3	3
Culista morsitans	0	2	2	0	0	2	0	2
Mansonia perturbans	718	325	1143	69	468	357	149	1043
	898	494	1392	114	620	465	193	1392

Table 15. Numbers of Culicidae Collected in Geometrical Targets of Two Colours Exposed at Various Strata (Study 2)

Height (cm)	Square			Pyramid			Grand Total
	Black	White	Total	Black	White	Total	
61	46	15	61	22	31	53	114
122	342	60	942	166	52	218	620
183	293	17	310	145	10	155	465
244	115	10	125	55	13	68	193
	796	102	898	388	106	494	1392

species (Table 14; Fig. 10).

A. punctor were taken from all heights but 37% of them from 122 cm and 28% from 183 cm. This species was more common at the 61 cm level (collecting 20% of the mosquitoes) than A. cantator of which 8% of the total was collected at this level. The traps at the 244 cm level collected 11% of the mosquitoes (Table 14; Fig. 10).

M. perturbans were collected at all strata but in low numbers at the 61 cm and 244 cm levels. This is consistent with the two Aedes spp. Forty-five percent of this species was taken from targets at the 122 cm level and 34% from the targets at 183 cm (Table 14; Fig. 10).

Chi-squared tests on all species result in $p < .01$ so the differences observed in the collections of mosquitoes of these three species at the various levels are significant. The information is supportive to Study 1 and 3 in which the targets were exposed at the 122 cm level. The results confirm the fact that the targets in the other studies were exposed at the most optimal level, in which a cross section of the mosquitoes could be found.

Study 3: Discrimination of Regions of Rectangular Targets

To further assess the use of vision in the orientation of Culicidae to hosts, a study was performed to determine the regional orientation of mosquitoes to rectangular shaped objects. This was accomplished by using rectangles that were partitioned internally into three compartments. The results of the study show a preferential response by mosquitoes for the end or projecting parts of the rectangle (Table 16). A chi-squared test, performed on the numbers of mosquitoes of each species collected from the three compartments results in $p < .05$, thus the results are significant and there is a differential response by the mosquitoes to the three

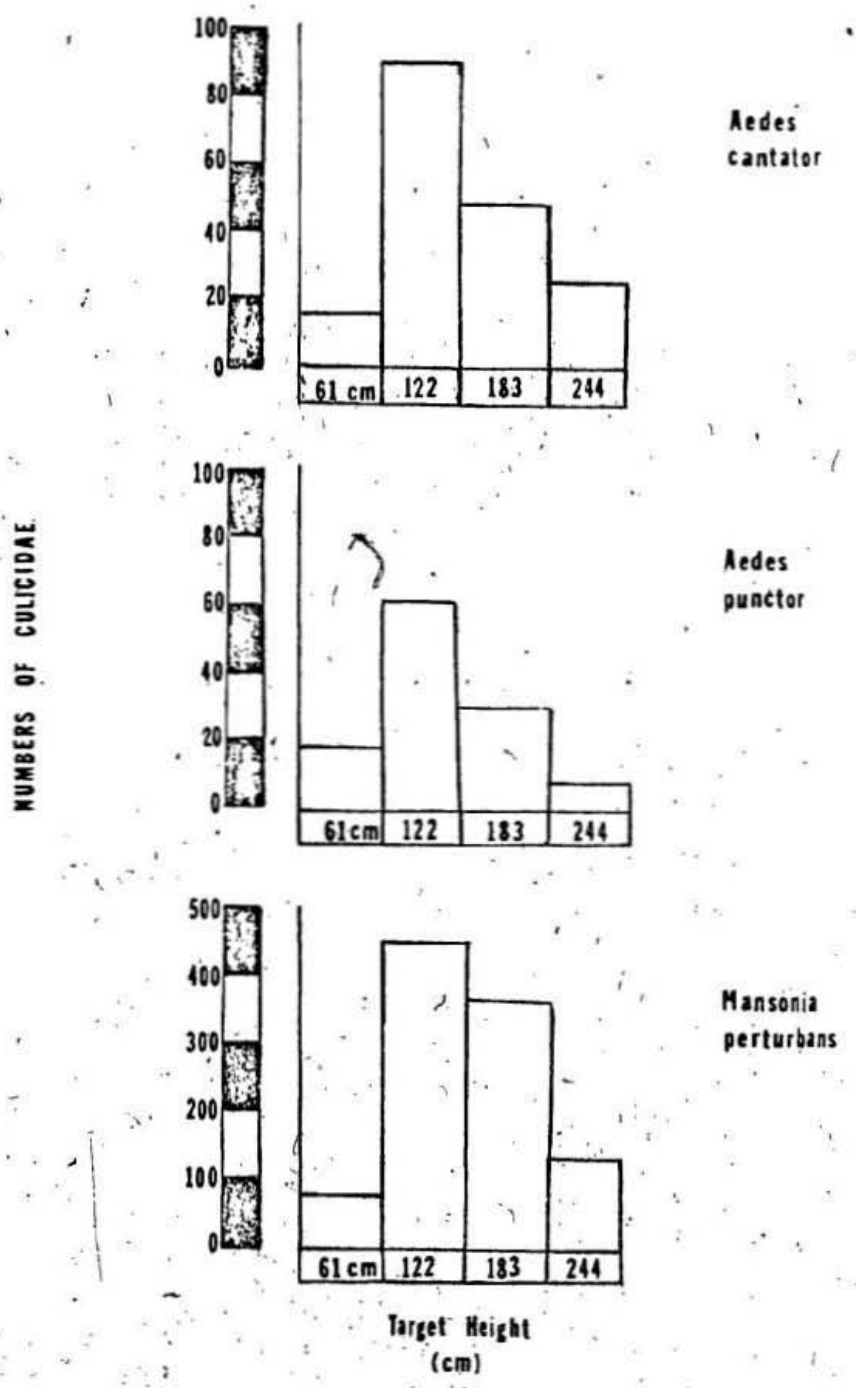

NUMBERS OF CULICIDAE
100
80
60
40
20
0
61 cm
122
183
244
Aedes cantator
Aedes punctor
500
400
300
200
100
Mansonia perturbans
Target Height (cm)

Table 16. Numbers of Culicidae Collected in the Three Regions of the Rectangular Targets (Study 3)

Species	Black E	Black C	Black E	Black Total	White E	White C	White E	White Total	Grand Total
Aedes canadensis	21	7	17	45	2	1	3	6	51
A. cantator	16	4	29	49	7	0	12	19	68
A. punctor	18	13	46	77	11	6	5	22	99
A. vexans	26	5	15	46	2	3	9	14	60
Mansonia perturbans	306	63	283	652	27	11	33	71	723
	387	92	390	869	49	21	62	132	1001

E = end, C = center

Summary of Chi-squared Tests

	Position 1, 2, 3 df 2	Position 1, 3 df 1
Aedes canadensis	*	***
A. cantator	**	*
A. punctor	**	***
A. vexans	**	***
Mansonia perturbans	**	***

* = $p<.05$

** = $p<.01$

*** = $p>.05$

compartments. Further chi-squared analysis on the numbers collected for each species from Positions 1 and 3 of each target show the results not to be significant and there was no difference in the numbers of mosquitoes collected from these two positions of the targets, except for A. punctor ($p<.05$). Summary of the chi-squared tests are in Table 16. The difference noted in the chi-squared analysis performed on each species for Positions 1, 2 and 3 is obviously due to the number 2 position. All species of mosquitoes, except A. punctor, are significantly selecting the two ends of the rectangles.

The influence of colour in the mosquitoes choice of a target was further assessed in this study. As in Studies 1 and 2, black targets collected greater numbers of mosquitoes than did the white targets (Table 16).

Study 4 Kodak Filter Study

Experiments to assess the spectral sensitivity of blood seeking M. perturbans females were carried out as two separate experiments as described in the materials and methods section.

Part A

To determine if the infrared component transmitted by the filters was influencing the response of the mosquitoes to the various filters, mosquitoes were offered a choice of two filters, one by itself and one paired with an infrared cut-off filter, #301, as outlined in Table 6. The infrared cut-off filter filters out near infrared radiation but transmits other wavelengths of the electromagnetic spectrum from 400-700 nm.

The scores in Table 17 are the numbers of landings on the filters for each of three trials. The results establish a differential landing

Table 17. Numbers of Mansonia perturbans landing on Kodak Filter Paired Experiment, Study 4, Part A, Trials 1, 2, and 3

Trial 1

Filter	47B + IRCO	61 + IRCO	92 + IRCO
47B	183	492	
	$p<.01$		
61	53	82	
	$p<.05$		
92	14	32	
	$p<.01$		

Trial 2

Filter	47B + IRCO	61 + IRCO	92 + IRCO
47B	109	311	
	$p<.01$		
61	44	152	
	$p<.01$		
92	20	37	
	$p<.05$		

Trial 3

Filter	47B + IRCO	61 + IRCO	92 + IRCO
47B	89	228	
	$p<.01$		
61	48	77	
	$p<.05$		
92	17	40	
	$p<.01$		
Totals	381	1031	
	145	311	
	51	109	

response to the filters combined with the infrared cut-off filter, indicating a selection by M. perturbans for the band of wavelengths without infrared radiation. A chi-squared test performed on each of the three trials of the paired filters (summarized in Table 17) indicates that there is a significant difference in the response of M. perturbans to the two bands of transmitted wavelengths.

Part B

The response of M. perturbans to the various wavelength bands of the electromagnetic spectrum, transmitted by the Kodak filters, when compared in pairs is summarized in Tables 18, 19 and 20, each table representing the results of one trial. The values given in the left column of the table are the actual number of landings and in the right column are the percentages of landing rate on the pair of filters. For example, in the comparison of filter 47B and 61 as shown in the top left hand corner of Table 18, the figures of 63 under filter 61 on the top line and of 37 under 47B on the second line are the percentages represented by a landing of 157 on filter 61 and 94 on filter 47B respectively. The percentages obtained by each filter against the other four filters are totalled at the bottom of the tables. The overall filter totals and percentages are given on the bottom of Table 20.

It is seen from Tables 18, 19, and 20 that filter 61 (peak wavelength 533.8 nm) was the most attractive filter followed by 47B (peak wavelength 452.7), 18A, 92 (peak wavelength 646.2) and 88A. The results are consistent throughout the three trials. Chi-squared tests performed on the three trials of each filter pair are significant. A summary of the Chi-squared test results are in Appendix 2.

Table 18. Numbers of Mansonia perturbans Landing on Kodak Filters Transmitting Narrow Wavelength Bands of Light, Paired Experiments Study 4, Part B, Trial 1

	Number of Landings on Filters									
Filter	47B		61		92		18A		88A	
	No.	%	No.	%	No.	%	No.	%	No.	%
47B	X		157	63	6	1	61	21	0	0
61	94	37	X		14	9	37	19	1	1
92	409	99	137	91	X		12	99	1	1
18A	231	79	157	81	1	1	X		6	3
88A	397	100	347	99	45	99	199	97	X	
Total	1131	315	798	334	66	110	309	236	8	5

Table 19. Numbers of Mansonia perturbans Landing on Kodak Filters Transmitting Narrow Wavelength Bands of Light, Paired Experiments Study 4, Part B, Trial 2

Filter	Number of Landing on Filters 47B		61		92		18A		88A	
	No.	%	No.	%	No.	%	No.	%	No.	%
47B	X		222	65	13	3	72	22	0	0
61	122	35	X		4	3	33	21	0	0
92	435	97	130	97	X		42	90	0	0
18A	251	78	123	79	10	10	X		0	0
88A	406	100	393	100	40	100	143	100	X	
Total	1214	310	868	341	67	116	289	233	0	0

Table 20. Numbers of Mansonia perturbans Landing on Kodak Filters Transmitting Narrow Wavelength Bands of Light, Paired Experiments. Study 4, Part B, Trial 3

Number of Landing on Filters

Filter	47B		61		92		18A		88A	
	No.	%	No.	%	No.	%	No.	%	No.	%
47B	X		171	66	16	16	97	97	0	0
61	107	34	X		3	3	18	19	0	0
92	411	96	103	97	X		12	85	1	1
18A	276	74	79	81	1	15	X		1	1
88A	441	100	300	100	37	100	167	99	X	
Total	1235	304	635	344	57	134	294	300	2	2

Total Number of Landings Per Filter and Total Percents

Filter	47B		61		92		18A		88A	
	No.	%	No.	%	No.	%	No.	%	No.	%
	3580	929	2319	1019	190	350	892	769	10	7

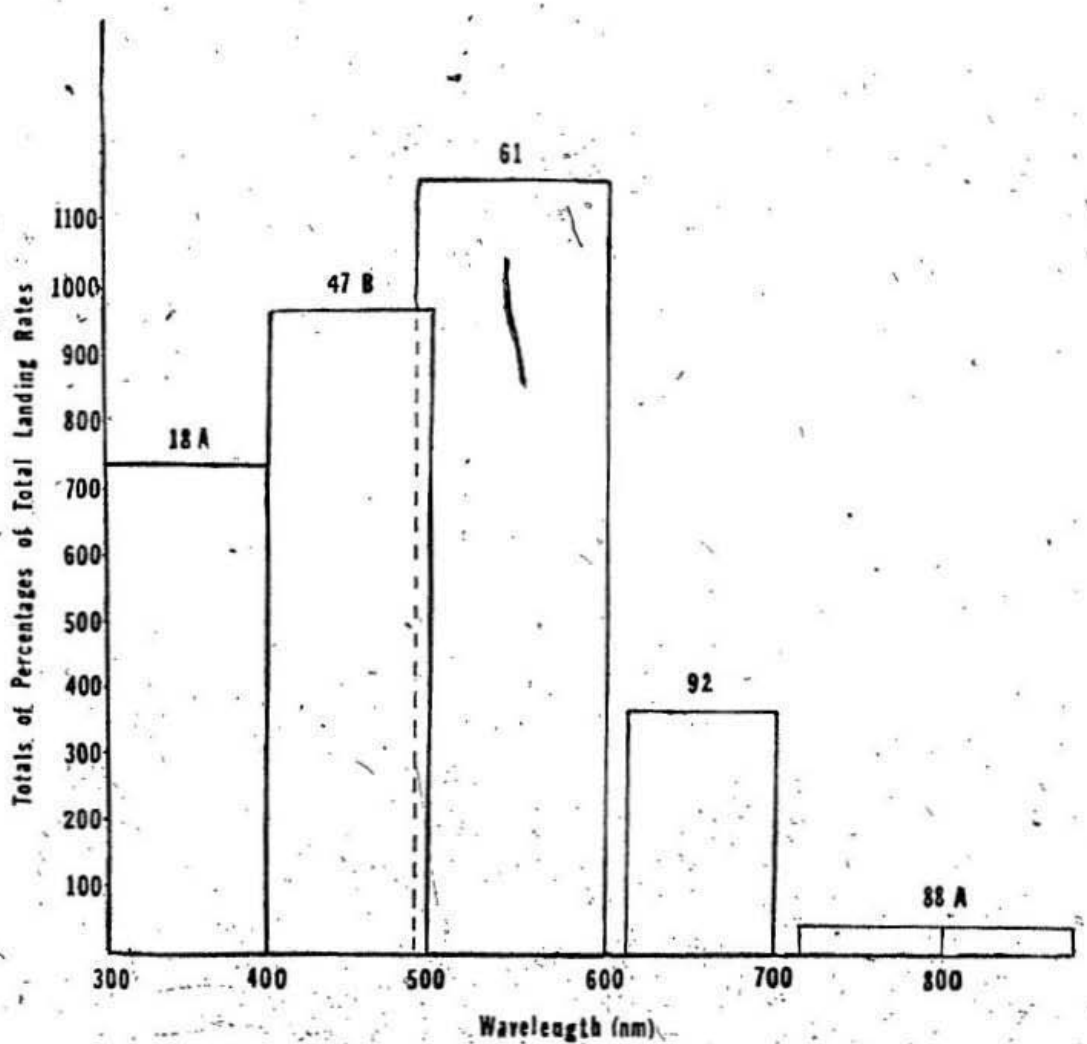
Further analysis using the Kendall Rank Correlation Coefficient of the ranked landing scores for the five filters over the three trials indicated a tau of 1.00 for trials 1 and 2, 2 and 3, and 1 and 3, indicating a high level of consistency in the order of attractance of the filters to M. perturbans between the series of trials.

With reference to Table 4 and Fig. 11 the results of Tables 18, 19 and 20 can be read in terms of transmitted wavelengths as opposed to filter numbers. The results show a differential landing response to the filters transmitting wavelengths of 480-600 nm and 400-555 nm, with the majority landing on the filter transmitting 480-600nm. This region of the spectrum is perceived by the human eye as a blue-green colour.

It is interesting to note the relatively high response to filter 18A which transmits wavelengths from 300-400 nm (ultraviolet radiation). This series of wavelengths is not perceived by the human eye. The visible spectrum for M. perturbans involves a definite shift to the left to include these wavelengths, as the results indicate (Fig. 11).

The results also establish that M. perturbans appeared to avoid infrared radiation. In Part B there were virtually no landings on the filters transmitting infrared radiation. This would seem to indicate that the mosquitoes were unable to visually perceive the wavelengths longer than 720 nm. However in Part A of the experiment the mosquitoes appeared to select the filters transmitting wavelength bands in the visible spectrum over filters transmitting wavelength bands with infrared radiation (Fig. 11).

Fig. 11 Response of Mansonia perturbans to the Electromagnetic Spectrum, (300-700 nm). Totals of Percentages of Landing Rates on the Kodak Filters Transmitting Narrow Wavelength Bands of the Electromagnetic Spectrum (Study 4B)


61
47 B
18 A
92
88 A
1100
1000
900
800
700
600
500
400
300
200
100
Totals of Percentages of Total Landing Rates
300
400
500
600
700
800
Wavelength (nm)

Discussion

Most of the previous investigations of the responses of Culicidae to coloured or other visual stimuli deal with A. aegypti, undoubtedly due to its ease of breeding in the laboratory. Observations on other genera and species are often extended to Culicidae, by analogy, with little regard to possible individual or species differences or to the physiological state of the mosquitoes being observed. Snow (1971) presents evidence that mosquitoes in the physiological state of searching for an oviposition site, respond differently to certain visual stimuli than those looking for a blood meal source. His experiments demonstrated that when A. aegypti were offered a choice between three oviposition sites, each illuminated by a different broad wavelength band, the site illuminated by wavelengths of 610 nm and longer (red) elicited the highest response (52% of eggs deposited). The 470-610 nm (green) site elicited the lowest (12%) and an intermediate number (36%) of eggs were deposited at the 360-500 nm (blue) site.

The responses of the mosquitoes to the various inanimate objects used in this study reflect an operative visual response in the mosquitoes' host-seeking behaviour. The response reflects a physiological process based on the need for a host blood meal which is imperative for ovarian development. It is assumed that mosquitoes, collected in this study, are in a common physiological state (blood-seeking) as a result of their response to CO_2. Carbon dioxide is widely employed as a releaser of the upwind oriented behaviour (Stage 2; Laarman, 1958), for most biting Diptera (Gillies and Wilkes, 1969; Snow, 1970). Kashin (1969) hypothesised the underlying olfactory mechanism by which mosquitoes locate their hosts. He proposed that gamma-aminobutyric acid (GABA), which is found in large

quantities in the nervous system of mosquitoes, is a synaptic inhibitor. His suggestion was that GABA combines with CO_2 (facilitated by atmospheric moisture) resulting in a carbamino-GABA compound. Uncombined GABA is a neuroinhibitor, but when activated by CO_2 (atmospheric moisture and perhaps even moisture from the blood meal host) the inhibitory power of GABA is diminished. He also suggests that activation with CO_2 may cause excitation or act as an irritant or noxious stimulus to the mosquito, thus the excitation causes the increased flight activity and upwind flight of the mosquito. The host stream of CO_2 keeps the mosquito constantly "primed" and "on target" (Kashin, 1969). Thus the long range orientation of the mosquito is mediated through olfactory cues. The CO_2 compressed gas released at each test site of the current study triggers and releases this upwind response. The visual responses to the targets reflect the visual responses operative in the near orientation (Stage 3) in the hierarchial host-seeking behaviour. With Stages 1 and 2 operative, then Stage 3 can be investigated resulting in Stage 4 or the landing stage (and subsequent trapping in targets).

The four separate studies performed in this paper were investigated to determine the capability of Culicidae to discern certain visual factors (shape, wavelength composition, etc.) as described by Laarman (1955, 1958) in the near-orientation to inanimate objects. One can then speculate on the extent to which mosquitoes utilize their visual sensory capacities in locating a blood meal source. Other factors underlying the response of female blood seeking mosquitoes (olfactory or chemical cues, physical cues) have been more extensively studied and have been reviewed elsewhere (cf. Laarman, 1955).

The Role of Wavelength Composition in the Choice of a Target

Howlett (1910), Eckstein (1920), Brighenti (1930), Gjullin (1947) and Headlee (1937) have established that mosquitoes have some degree of colour perception but it is unclear exactly which wavelengths of the spectrum they perceive and whether they can distinguish them when they are presented simultaneously.

In the coloured artboard study, three species, A. cantator, A. punctor and M. perturbans (Tables 8 and 9) were shown to respond differentially to the five artboards of different wavelength compositions. These artboards are seen by the human eye as black, red, blue, white and yellow. The results for these three species in 1977 and 1978 (Figs. 7 and 8) repeatedly show greater numbers of aedines and M. perturbans from the black, red and blue target traps, and low numbers on yellow and white traps. The percentages of each species collected from the black, red and blue fluctuate so that it is difficult to separate these three artboards on the basis of mosquito attraction. Although the overall totals establish black as the most attractive artboard, followed by red and then blue, the individual species totals do not. In 1978, black received equal numbers of M. perturbans as blue. In 1977 it received fewer numbers of A. cantator than blue. Similar fluctuations exist for white and yellow. Although they are unattractive artboards yellow was more attractive than blue for A. punctor and white collected approximately equal numbers as blue for M. perturbans in 1977.

As a result of these fluctuations, one colour can not be concluded as more attractive than another. More accurately the results indicate a grouping of artboards so that black, red and blue are more attractive than white and yellow. This is consistent for aedines and M. perturbans.

From the spectral analyses of the artboards in Table 1, it is apparent that the three species are responding in greater numbers to the boards reflecting peak wavelengths of 450 nm (blue) and reflecting a range of wavelengths from 580-700 nm (red). Wavelength measurements are not given for the black and white artboards, as theoretically the black artboard absorbs all wavelengths of light incident upon it and the white artboard reflects all wavelengths of light.

In interpreting the present results, it was considered that the percentage of light reflected from the artboards might have been the cause of any preference or dislike shown by the mosquitoes. Such a theory is well documented for Simuliidae (Davies, 1972; Bradbury, 1972). This type of trend seems to suggest that the attractiveness of an object is influenced more by the intensity than by the wavelength of the reflected light such that when the total intensity of the light reflected from the coloured objects is high, few flies land but when the intensity is low more flies land. This is interpreted as a self protective move on the part of the insect to avoid high intensities of light. The landing responses of Culicidae as a function of percent luminous reflectance of the artboards illustrates that, generally in 1978, the percentages of luminous reflectance of the various artboards are inversely proportional to the numbers of Culicidae being trapped in the targets (Fig. 9). In other words, a decrease in the luminous reflectance or the artboard reflecting the least amount of light increases the mosquito catch or attraction. There were exceptions in 1977. White attracted more than yellow even though white had a higher luminous reflectance. In 1978, the trend was further concealed by red attracting more mosquitoes than blue even though blue had a lower luminous reflectance. The same type

of inconsistencies existed for the aedines and M. perturbans. The fact that there are substantial discrepancies in the present data perhaps indicate that intensity is not the only factor in selection of a coloured object and perhaps not the primary one.

There are certain limitations with using coloured artboards when trying to determine the area of the spectrum to which mosquitoes are sensitive. This approach results in only approximate information on the visual phenomena, as limited spectral information is available. The peak wavelengths or bands of wavelengths given for the different artboards give an indication of the wavelengths that the mosquitoes are responding to but as Table 2 indicates, the artboards reflect wavelengths of varying intensities throughout the entire spectrum from 350-700 nm. The intensity of reflected light from the artboards (Table 2) is highest near the peak wavelengths of the boards which further complicates the interpretation of data. It is difficult to establish whether the response is to the intensity or to the peak wavelengths of the reflected light.

In 1938, Brett concluded that A. aegypti preferred darker coloured clothing over lighter ones. Of those cloths examined, the species preferred black to anything, red was next and it apparently disliked blue. Of the lighter colours, light-yellowish khaki attracted fewer flies than white. The preference for colours agrees with the present results, however Brett (1938) gives no indication of spectral data of the reflected wavelengths of the cloths. Comparison of his results to the present ones is difficult, since the colour of an object does not always fully characterise the wavelength composition. Colours can look alike yet be of different spectral compositions, such as in the case of monochromatic yellow and yellow composed of combinations of wavelengths seen as

green and red. For this reason two objects of apparently the same colour may excite an insects' eye to different degrees and thus influence differently the animals' behaviour. Brett (1938) further interprets his results by looking at the percentage reflection factors of the different coloured cloths. His mosquitoes preferred surfaces with a low reflection factor. This is in agreement with the current observations but he too observed that red was more attractive than several colours with a higher reflection value. Except for experimental error he offers no explanation of these findings.

Brown (1951, 1954) observed Aedes spp. and their attraction to different cloths. He noticed black to be more attractive than any other cloth, followed by red, blue, brown, green, white and yellow, an observation similar to Brett (1938) and the current results. Again no spectral data was given. He observed that the attractiveness of a cloth as a landing surface for female adult mosquitoes is an inverse function of its reflectivity for light between 475 and 635 nm. He also noticed exceptions to this. He attributes these as being a result of the texture of the cloths which obscurred the generalisation of the importance of intensity of reflected light in attraction of an object. His other explanation was associated with the floristic setting (which was a spruce forest) where the experiments were conducted. In his experiments the green cloths were less attractive than their low reflectivity would seem to warrant and he attributes this to them being masked in the green setting. On the other hand, the bright red cloths (also with low reflectivity), owing to their conspicuousness in the green setting, were quite attractive. The idea of simultaneous contrast is well known for other insects so this could well be influencing the mosquitoes in

their choice of the red target over the green target in Browns' (1951, 1954) results. This could well be an explanation of the discrepancies in the current observations owing to the similarity of the test sites to Browns'.

Gilbert and Gouck (1957) compared A. aegypti, A. taeniorhynchus and A. sollicitans in two experiments. In the first they compared intensities (measured in footcandles) of the same colour. A. aegypti was the only species in which the lower intensities of any colour were progressively more attractive than the higher intensities. The landing rate of A. taeniorhynchus was the reverse of A. aegypti. The highest intensity of each colour had the greatest landing rate. A. sollicitans preferred the lower intensities of yellow, red and orange, and the higher intensities of the darker colours (blue). These results are contrary to Brett (1938) and Brown (1951, 1954) and the present observations. The colour choice of his mosquitoes in his second experiment are contrary to all other observations as well. When colours of equal intensities were exposed to the mosquitoes the following resulted:

A. aegypti	40 foot candles	Yellow $>^{*}$ orange, and red > green, violet, black blue and white
	20 foot candles	Orange and red > violet, black, green and blue > white
A. taeniorhynchus		
	40 foot candles	White > orange, green, yellow and blue > violet, red and black
	20 foot candles	White > green and black > blue and violet > red and orange

*significantly more attractive than.

A. sollicitans

40 foot candles — Black, blue, orange and green > yellow, violet, red and white

20 foot candles — no significant differences in the colours. The order of attractiveness was: Black, green, orange, violet, red and blue.

As no spectral data on the wavelengths of the colours was given, it is again difficult to compare these results with other observations. The A. aegypti results do not compare with those given by Brett (1938). Although the other two species of Aedes were not studied previously, the results do not agree with other Aedes spp. observations given by Brown (1951, 1954), or the present observations. Gilbert and Gouck's (1957) results could possibly indicate species differences, however their results must be considered with caution. The authors neglected to determine the physiological state of the mosquitoes except that they were adult. The population could conceivably have been a mixture of ovipositing and host-seeking mosquitoes. Considering Snow's (1971) observations, this could well have affected the results. Also it was stated that the population consisted of males and females in undetermined sex ratios. The results could also reflect differences in the visual responses of the sexes to coloured objects.

Although the colour preference results of Gilbert and Gouck (1957) are contrary to other results, they do in fact establish one interesting point. The mosquitoes were able to distinguish wavelengths independent of intensity as is seen in the results of their second experiment where intensity of all the colours was the same. This is evidence that these three aedines have colour vision. Brett (1938) compared two colours (black and brown) of equal intensities and showed that A. aegypti landed

in greater numbers on the brown cloth. He concluded that this species does have a colour sense and prefers brown to black. Frost (1954) showed families of insects (including Culicidae) to respond in greater numbers to UV wavelengths than to longer wavelengths of equal intensities.

Colour vision is defined as the ability to distinguish colours according to their wavelength composition at any intensity. Ever since von Frisch (1958) demonstrated this for bees through a conditioned reflex, the question has remained whether other insects have this ability. Not all insects develop strong conditioned reflexes toward discrimination of visual stimuli. Mazokhin-Porshnyakov (1969) points out that insects, such as biting flies, establish reflexes with difficulty and which disappear in a few hours. Alternatively, demonstration of colour vision in mosquitoes is established by recording differential responses of the mosquitoes to different wavelength compositions at the same intensity. Except for the observations of Brett (1938) and Gilbert and Gouck (1957) no further evidence of colour vision exists for Culicidae, indicating the need for further study.

Some authors maintain that if the vital needs of mosquitoes and other insects are strongly dependent on their visual recognition of an object, then they will rely on the most constant form of recognition (Goldsmith, 1961; Mazokhin-Porshnyakov, 1969). It would seem of more benefit to the mosquitoes to have developed their visual sense to perceive objects by its ability to reflect wavelengths and not by the intensity of the reflected light, as this varies with illumination. The wavelength composition of light reflected by an object in different conditions of illumination differs also. For example, a yellow flower in the shade reflects almost all green rays, since in the shade of green trees the

light diffused from the sky contains only a small amount of yellow-red radiation. In the open, the flower reflects more yellow-red radiation than green. Humans see the flower as yellow in both conditions due to their colour compensating mechanism (Helmholtz Theory, cf. Newberg, 1960). Insects too must possess this mechanism of colour constancy for without it, they could not recognise objects when they are differently illuminated. It would seem of more benefit to mosquitoes seeking a blood meal, to distinguish objects from one another on the basis of how the objects reflect wavelengths, rather than on the intensity of reflected light as the former is a more constant factor, assuming the colour compensating mechanism exists. In this way, the mosquitoes would be able to recognise an avian or mammalian host regardless of the intensity of the reflected light. This can only be shown exclusively by giving the mosquitoes a series of objects reflecting different bands of wavelengths, all of the same intensity and having the mosquitoes select narrow bands of wavelengths independent of intensity. This would show the insect to have a colour sense or colour vision by the definition. It may well be that there is an interaction of wavelength and intensity in the mosquitoes choice of an object. It could be that mosquitoes primarily respond to wavelength and then secondarily to the object reflecting the lower percentage of light as it is to the mosquitoes advantage to avoid high intensities of light.

The question whether nocturnal species are able to discern wavelengths is partially explored in this study. Literature is scarce on this subject for Culicidae. The weak illumination present at night creates more difficult conditions for the colour vision apparatus. To function, it must possess enhanced absolute and contrasting sensitivity

to light but from the physical standpoint this is difficult to combine with colour differentiation. The present results indicate that M. perturbans is able to differentiate certain of the coloured artboards in the night. Whereas at day, the species discriminated black (collected 57%) from blue and red (16 and 18% respectively) from white and yellow (5 and 4%); at night, black and blue attracted very similar numbers of the species (34 and 31%). White, which was unattractive in the day was more attractive than blue in the night. Yellow was not attractive at day or night, and red occupied an intermediate level of attractiveness in the night as in the day.

Mazokhin-Porshnyakov (1969) observed that in nocturnal insects (moths: Cosmotriche potatoria, Hepialus sylvanus, Parastichtis lateritia and the beetle Prionus coriarus) at illuminations of 2 luxes, the eyes are able to distinguish fairly disparate spectral wavelengths. As varying reductions in illumination occur, the eyes gradually lose the capacity to distinguish wavelengths close in proximity. Illumination under natural conditions at night will not exceed 0.2 lux (full moon). On a clear moonless night the illumination is about 0.0003 lux. For each species, the level of threshold at which the species could no longer distinguish wavelengths differed but some degree of night vision was observed. The explanation given for the enhanced sensitivity of the eye with the onset of evening is that the protective colour pigments migrate from the day time position to the night time position providing a wider access of light to the optic cells (Yahn and Crescitelli, 1940; Bernhard and Ottoson, 1960, 1961). Thus far, it has been established that mosquitoes are able to discern coloured artboards at day and night but due to the complication involved with the use of coloured objects it is difficult

to say whether the mosquitoes are selecting the objects by their reflected wavelengths or by the percent luminous reflectance.

The Kodak filter experiment results indicate more precisely than the coloured artboard study, the area of the spectrum that the mosquitoes' visual system is able to perceive. Response of M. perturbans (in decreasing order of attraction towards the filters) was: filter 61 (wavelengths of 480-600 nm); filter 47B (wavelengths of 400-480 nm), filter 18A (wavelengths of 300-400 nm), and filter 88A (720 nm and longer wavelengths - infrared; Fig. 11). The peak activity of mosquitoes studied by Delong (1954) was not within the 480-600 nm range found in this study but in the 364-400 nm range (ultraviolet).

The filter data is more comparable to electrophysiological results than is the coloured artboard data. Electrophysiological results are obtained by planting electrodes in the visual cells or ommatidia of the compound eyes and recording intracellular changes which occur when a beam of light of known wavelengths is focused on the eye. The results are in the form of an electroretinograph (ERG) which indicates, by peaks, the spectral sensitivity of the visual pigments present. Mainly, species of Calliphora and Musca (Cyclorrhapha) of the Diptera have been studied for their spectral response curves using electrophysiological techniques (Eckert, 1970). Members of both genera show almost identical curves. The ERG holds four developed peaks at 360, 460, 490 and 620 nm. The peak at 620 nm is attributed to red light radiation transparency of the screening pigments (Burkhardt, 1962; Goldsmith, 1965). The peak at 490 nm reflects the principal absorption peak of a green receptor system localized in visual cells 1-6. The maxima at 460 nm reflects the principal absorption peak of the blue receptor system localized in visual cells 7 and 8 (Langer, 1965). Minor maxima of both receptor systems in the

ultraviolet contribute to peak 360 nm (Burkhardt, 1962). Comparison of this data with the Kodak filter study results shows the peaks of response by M. perturbans to be closely similar to the ERG peaks of the dipterans previously examined. The ERG of other dipterans, e.g., Eristalis spp. (Cyclorrhapha; Autrum, 1952; Schatz, 1971), Bibio spp. (Nematocera; De la Motte, 1972) appear very similar. The importance of having recordings of behavioural responses to visual stimuli for comparison with ERG is emphasized, as electrophysiological studies do not reflect the insects' ability to utilize the potential of the visual pigments present, e.g., the visual pigments of vertebrates have a significant sensitivity to the near ultraviolet as determined from eletrophysiological studies. However the yellow lenses of vertebrates tend to prevent ultraviolet from reaching the visual cells (Wald, 1958). This restriction was probably introduced in the vertebrate eye to relieve chromatic aberration, a problem not met in compound eyes.

Burkhardt and De la Motte (1972) sum up their findings by saying that of the dipterans studied there is evidence for the existence of a short and a long wavelength receptor system. The occurrence of a green receptor system seems to be typical, the main maxima lying between 490-520 nm, accompanied by a minor maxima in the ultraviolet. In addition, a short wavelength receptor is present with a peak at 360 nm or between 430 and 460 nm. It appears that Diptera have the prerequisites for dichromatic colour vision; however further receptor systems may be involved for other species.

For the Kodak filters, the intensity of light coming through the filter is expressed in terms of the percentage of luminous transmittance and not luminous reflectance as for the artboards. In this case the

filter transmitting the highest luminous value, ie., 16.8% (61) was the most attractive filter. This finding is contrary to all previous observations in which the lower numbers were collected from the objects with the highest intensity. The filter transmitting the lowest intensity was 47B, the second most attractive filter. The unattractive 92 had an intermediate level of percentage luminous transmittance. This does not coincide with the idea expressed previously that a mosquitoes' visual response to a coloured object is determined primarily by the brightness and not the reflected wavelengths. This could be used as an argument in support of wavelength being selected over intensity.

As the results of the filter experiment show M. perturbans has a wider visible spectrum than humans, such that it includes near ultraviolet wavelengths (300-400 nm). Such a phenomenon has been observed for other insects as well. It has been suggested that this phenomenon enables insects to distinguish objects in nature which reflect ultraviolet wavelengths (Mazokhin-Porshnyakov, 1969). Results show that for the plants, flowers and insects studied reflections of ultraviolet wavelengths are in small amounts (<10%) but are different enough for the objects to be distinguished by an organism that is able to perceive ultraviolet light (Lutz, 1933; Brues, 1941; Mazokhin-Porshnyakov, 1954). Photographs taken in ultraviolet light (by these authors) show that butterflies do not appear as we see them under normal light. Sexual differences exist in the colours of butterfly bodies, due to unequal absorption of ultraviolet light. Mazokhin-Porshnyakov (1954) list numerous plants and insects for which differences in ultraviolet absorption and reflection occur. Daumer (1958) has demonstrated that honey bees are able to guide their search for nectar by the different patterns

of ultraviolet light reflected from the plants. It is conceivable that the ability of the mosquitoes to perceive the near ultraviolet radiation (detected in the current filter study) is used in distinguishing animals in nature as potential blood sources. Mammals or birds may well reflect ultraviolet radiation in different degrees as plants and insects do. This would make them more conspicuous to the mosquitoes against the background vegetation.

The filter experiment also established that M. perturbans does not respond to wavelengths in the infrared region of the spectrum. They apparently perceive these wavelengths, as indicated in Part A of the filter study, where the mosquitoes landed in greater numbers on the filters without the infrared component transmitted through the filter. This relatively low response to the infrared radiation supports Peterson and Brown (1951) and Brown (1954), who observed no correlation between attractiveness of an object and infrared radiation.

The Role of Shape in the Visual Near Orientation and Landing of Culicidae

The results of this study indicate that of the two, three-dimensional shapes, cubes were significantly more attractive than pyramids (Table 13). Black cubes were eight times more attractive than white cubes and the black pyramids were four times more attractive than white ones, indicating colour to be of more influence in the choice of a target than shape.

Cubes were significantly different from pyramids in their individual contours to elicit specific responses among two culicids (A. cantator and M. perturbans). A. punctor was taken more frequently from pyramids but the differences in the numbers collected from cubes and pyramids were not as pronounced as for the other two species.

The shape of the target traps in the other studies was a cube and it is believed that this shape was appropriate for collections owing to its proven attractiveness in study 2 and because it attracted large numbers of flies throughout the collection periods. A. punctor, which preferred pyramids, was collected in relatively large numbers from cubes in the colour preference study.

The current explanation of discrimination of geometrical shape by insects (Mazokhin-Porshnyakov, 1969), is that when an insect such as a mosquito is flying, a given object presents itself as a sequence of stimuli in the form of light flashes, which reach the ommatidia and give rise to successive changes in excitation of the appropriate visual cells. The number of flashes is a function of the structural aspects of the object and of irregularities of its contour. A cube would elicit a greater reponse than a disc for example. The more broken the pattern of an object the higher the stimulation reaching the faceted eye. Mazokhin-Porshnyakov and Vishnevskoya (1965) point out that it is possible to mask such a response if the objects are too big. This was apparently the case in the work of Tsuneki (1961) with bees. If the objects are too large relative to the size of the insect, the insect cannot see the whole contours of the objects at close distances. This indicates perhaps that the discrimination of objects in this study was made while the insect was still in flight and hovering about the target, so that when the mosquitoes landed, the targets appeared as enormous black and white objects, hindering any further shape discrimination. No literature exists on shape discrimination in mosquitoes. A. cantator and M. perturbans seemed to prefer the objects with extensive contours (cubes) while A. punctor was attracted more by the objects with fewer contours.

Somewhat related to the importance of contour is the observation by Brown (1952) who used cardboard cubes containing equal amounts of black and white in a checkerboard or striped pattern. The more contours present (by way of increased pattern), the more mosquitoes were attracted.

Henk and Schlörer (1963) found that Wilhemia spp. preferred projecting parts (e.g., ears of horses or cows) of silhouettes when seeking a blood meal. They also noticed that some ornithophilic species preferred small avian targets with projecting parts (e.g., necks). This point is well documented for Simuliidae (Peschken and Thorsteinson, 1965; Bennett, et al., 1972; Bradbury, 1972; Browne and Bennett, 1979). Fallis et al. (1967) collected more simuliids from the end portions of sticky cylindrical silhouettes than from the mid-portions. It appears that various points of convergence of targets are favoured landing sites for host-seeking simuliids. This was investigated for Culicidae in the current study. Four species of Aedes and one species of Mansonia were collected in significantly different numbers from the ends of the rectangular targets than from the center. This coincides with existing observations that some biting flies seek the points of convergence of objects as they associate this with areas of a hosts' body where a blood meal could be easily obtained (e.g., the ears or the neck of an animal) as compared to the center of an animals' body.

Stratification

The targets of the shape preference study were exposed at various strata to collect species of mosquitoes that might have been vertically stratified in the environment. Although targets at the levels examined did not collect certain species exclusively, targets exposed at levels of 122 and 183 cm collected more aedines and Mansonia than did the lower

and higher targets. This indicates that these levels are the optimal feeding strata for these species. This is also evidence that the traps used in the other studies were exposed at the most opportune levels to collect large numbers of mosquitoes.

The vertical distribution of mosquitoes has been investigated in many parts of the world, such as Africa, because of the importance of sylvan yellow fever (Haddow, et al., 1947; Mattingly, 1949; Corbet, 1961). Similar studies were carried out by Gillies and Wilkes (1974) and Snow (1975) in areas of the Gambia. In Georgia, numerous authors have reported finding vertical distribution levels for various genera of Culicidae (MacCreary, 1941; Gjullin, et al., 1950; Snow, 1955; Love and Smith, 1958). In the majority of studies, correlations between the indicated vertical distribution and the known feeding preferences on hosts are discussed. The literature does indicate natural stratification of mosquito species, thus Study 2 was not an attempt to establish stratification but an attempt to sample various strata to include possible stratified species in the results.

Some authors have suggested practical application of colour preference information as a means of personal protection against mosquitoes. A practical recommendation is the change from dark coloured to light coloured dress when exposed to biting flies. This would include wearing clothing that reflects a series of wavelengths proven not to be attractive to biting flies as well as clothing that has a high luminous reflectance. It must be realized that such action alone will not effectively deter biting flies. Applications of repellents combined with the proper clothing will further reduce the numbers of biting flies about the body. It is insufficient to apply the repellents just to the exposed areas of the body as heat convection currents through clothes are

enough to attract the flies. The clothes should be impregnated with the repellent as suggested by Travis and Morton (1946), Smith and Cole (1951), and Schreck, et al. (1977).

In the course of this study it was realized the need for standardization of protocols to enable more accurate comparisons of data from different studies. The results also indicate a need for further study to establish more precisely the wavelengths of the spectrum that the mosquitoes are able to perceive. This could be accomplished by further Kodak Filter experiments in which filters of narrower wavelength bands are used. Incorporation of a control of intensity for the light transmitted through the filters would establish whether or not mosquitoes have the ability to distinguish wavelengths of the same intensity (colour vision)! Intensity could be varied as well to determine if the mosquitoes respond differentially to different levels of intensity. Further study into the mosquitoes' ability to perceive ultraviolet light would be useful to establish whether they use the reflected ultraviolet light from objects to distinguish them in nature. Ultraviolet light photographs of potential blood sources would also provide useful information.

Literature Cited

Autrum, H. 1952. Ueber zeitliches Auflosungsvermogen und Primarvargange im Insektenauge. Naturwissenschaften 139: 290-297.

Bennett, G.F. 1960. On some ornithophilic blood-sucking Diptera in Algonquin Park, Ontario, Canada. Can. J. Zool. 38: 377-389.

_____, A.M. Fallis and A.G. Campbell, 1972. The response of Simulium (Eusimulium) euryadminiculum Davies (Diptera:Simuliidae) to some olfactory and visual stimuli. Can. J. Zool. 50: 793-800.

Bernhard, C.G. and D. Ottoson, 1960. Studies on the relation between the pigment migration and the sensitivity changes during dark adaptation in diurnal and nocturnal Lepidoptera. J. Gen. Physiol. 44: 205-215.

_____, 1961. Further studies on the pigment migration and sensitivity changes in the compound eye of nocturnal insects. Acta Physiol. Scand. 52: 99-100.

Bradbury, W.C. 1972. Experiments and Observations on the Near Host Orientation and Landing Behaviour of Simuliidae (Diptera). M.Sc. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland. 139pp.

_____, and G.F. Bennett, 1974. Behaviour of adult Simuliidae (Diptera II). Vision and olfaction in near-orientation and landing. Can. J. Zool. 52: 1355-1364.

Brett, G.A. 1938. On the relative attractiveness to Aedes aegypti of certain coloured cloths. Trans. R. Soc. Trop. Med. Hyg. Vol. XXXII. No. 1 (June): 113-124.

Breyev, K.A. 1963. The effect of various light sources on the numbers and species of blood-sucking mosquitoes (Diptera, Culicidae) collected in light traps. Entomol. Rev. 42: 155-168.

Brighenti, D. 1930. Ricerche sulla attrazione esercitata dai calori sugli anofeli. Riv. Malariol 9: 224.

Brown, A.W.A. 1951. Studies on the responses of the female Aedes mosquito. Part IV: Field experiments on Canadian species. Bull. Entomol. Res. 42: 575-582.

_____, 1952. Factors in the attractiveness of bodies for mosquitoes. Trans. Ninth Intn. Congr. Ent. 1: 895-900.

_____, 1954. Studies of the responses of the female mosquito. Part VI: The attractiveness of coloured cloths to the Canadian species. Bull. Entomol. Res. 45: 67-78.

Browne, S.M. and G.F. Bennett, 1979. Color and shape as mediators of the host-seeking behavior of Simuliids and Tabanids in the Tintamirre National Wildlife Area, New Brunswick. J. Med. Entomol. (In Press).

Brues, C.T. 1941. Photographic evidence on the visibility of color pattern to the human and insect eye. Proc. Amer. Arts and Sci. 74: 281-285.

Burkhardt, D. 1962. Spectral sensitivity and other response characteristics of single visual cells in the arthropod eye. Symp. Soc. Exp. Biol. 16: 86-109.

_____, and De la Motte, 1972. Electrophysiological studies on the eyes of Diptera, Mecoptera, and Hymenoptera. Symposium at the Dept. of Zool., Univ. of Zurich, March 6-9. Information Processing in the Visual Systems of Arthropods.

Carpenter, S.J. and W. J. LaCasse, 1955. Mosquitoes of North America (North of Mexico). Univ. of Calif. Press, Berkeley, Calif.

Corbet, P.S. 1961. Entomological studies from a high tower in Mpanga Forest Uganda. VI: Nocturnal flight activity of Culicidae and Tabanidae as indicated by light traps. Trans. R. Entomol. Soc. Lond. 113: 301-314.

Dampier, W.C. 1948. A History of Science and its Relations with Philosophy and Religion. Cambridge Univ. Press (fourth ed.). Cambridge England. 527pp.

Daumer, K. 1958. Blumenfarben, wie sie die Bienen Sehen. Z. Vgl. Physiol. 41: 49-110.

Davies, D.M. 1972. The landing of blood-ssking female blackflies (Diptera: Simuliidae) on coloured material. Proc. Entomol. Soc. Ont. 102: 124-155.

_____, and B.V. Peterson, 1957. Black flies over lakes (Simuliidae:Diptera). Ann. Entomol. Soc. Am. 50: 514-521.

Delong, D.M. 1954. Fundamental studies on behavior of larval and adult mosquitoes and evaluation of mosquito repellents. Ohio Engin. Exp. Sta. News 26: 51-55.

Dethier, V.G. 1947. Chemical Insect Attractants and Repellents. H.K. Lewis and Co., London.

Eckert, H. 1970. Diss. Freie Univ. Berlin (zit. n. Kirschfeld). Naturwissenschaften 58: 201-209.

Eckstein, F. 1920. Aus einer Felststion fur Steckmucken. Z. angew. Entomol. 6: 338.

Fallis, A.M., G.F. Bennett, G. Griggs and T. Allen, 1967. Collecting Simulium venustum females in fan traps and on silhouettes with the aid of carbon dioxide. Can. J. Zool. 45: 1101-1107.

Fedder, M.L. and A.N. Alekseyev, 1965. [Optic reaction of certain blood-sucking Diptera (Insecta) to various colors.] Entomologiccheskoe Obozrenie 44: 293-296.

Frisch, von, K. 1958. Bees: Their Vision, Chemical Senses and Language. Great Seal Books, Cornell Univ. Press, Ithaca, N.Y. 118pp.

Frost, S.W. 1954. Response of insects to black and white light. J. Econ. Entomol. 47: 275-278.

Gilbert, I.H. and H.K. Gouck, 1957. Influence of surface color on mosquito landing rates. J. Econ. Entomol. 50: 678-680.

Gillies, M.T. and T.J. Wilkes, 1969. A comparison of the range of attraction of animal baits and of carbon dioxide for some West African mosquitoes. Bull. Entomol. Res. 59: 441-456.

_____, 1974. The vertical distribution of mosquitoes flying over open farmland in the Gambia. Trans. R. Soc. Trop. Med. Hyg. 68: 268-269.

Gjullin, C.M. 1947. Effect of clothing color on the rate of attack of Aedes mosquitoes. J. Econ. Entomol. 40: 326-327.

_____, W.W. Yates and H.H. Stage, 1950. Studies on Aedes vexans (Meig.) and Aedes sticticus (Meig.) floodwater mosquitoes in the lower Columbia River Valley. Ann. Entomol. Soc. Am. 43: 262-275.

Goldsmith, T.H. 1961. The color vision of insects. In - W.D. McElroy and B. Glass (eds.), A symposium on Light and Life. The Johns Hopkins Press, Baltimore. pp. 771-794.

_____, 1965. Do flies have a red receptor? J. Gen. Physiol. 49: 265-287.

Golini, V. 1970. Observations on Some Factors Involved in the Host-Seeking Behavior of simuliids (Diptera) in Ontario and Norway. M.Sc. Thesis, McMaster Univ. Hamilton, Ontario. 230pp.

Haddow, A.J., J.D. Gillett and R.D. Highton, 1947. The mosquitoes of Bwamba county, Uganda. V. The vertical distribution and biting cycle of mosquitoes in rain-forest, with further observations on microclimate. Bull. Entomol. Res. 37: 301-330.

Haufe, W.O. and L. Burgess, 1960. Design and efficiency of mosquito traps based on visual response to patterns. Can. Entomol. 92: 124-140.

Headlee, T.J. 1937. Some facts underlying the attraction of mosquitoes to sources of radiant energy. J. Econ. Entomol. 30: 309-312.

Herman, C.M. and G.F. Bennett, 1976. Use of sentinel ducks in epizootiological studies of anatid blood protozoa. Can. J. Zool 54: 1038-1043.

Hocking, B. 1971. Blood-sucking behaviour of terrestrial arthropods. Annu. Rev. Entomol. 16: 1-26.

Howlett, F.M. 1910. The influence of temperature upon the biting of mosquitoes. Parasitology 3: 477.

Kashin, P. 1969. The role of gamma-amino butyric acid in mosquito host interactions: A hypothesis. Ann. Entomol. Soc. Am 62: 695-702.

Kellogg, F.E. and R.H. Wright, 1962. The guidance of flying insects. V. Mosquito attraction. Can. Entomol. 94: 1009-1016.

KODAK Publication B3. Kokak Filters for Scientific and Technical Uses. Kodak Publ. No. B3. Eastman Kodak Co. Rochester, N.Y.

Laarman, J.J. 1955. The host-seeking behaviour of the malaria mosquito Anopheles maculipennis atroparvus. Acta Leidensia 25: 1-144.

_____, 1958. The host-seeking behavior of Anopheline mosquitoes. Trop. Geogr. Med. 10: 293-305.

Langer, H. 1965. Spektrometrische Untersuchung der Absorptionse igenschaften einzelner Rhabdamere im Facettenauge. Verh. dt. Zool. Geo; Jena, Zool. Anz. Suppl. 29: 329-338.

Lewis, D.J. 1976. The Biting Flies of the Nova Scotia - New Brunswick Border Region. Ph.D. Thesis, Memorial Univ. of Newfoundland. St. John's, Newfoundland. 238pp.

Love, G.J. and W.W. Smith, 1958. The stratification of mosquitoes. Mosq. News 18: 279-283.

Lutz, F.E. 1933. "Invisible" colors of flowers and butterflies. J. Am. Mus. Nat. Hist. 33: 565-576.

MacCreary, D. 1941. Comparative density of mosquitoes at ground level and at an elevation of approximately one hundred feet. J. Econ. Entomol. 34: 174-179.

Mattingly, P.F. 1949. Studies on West African forest mosquitoes. Part I: The seasonal distribution, biting cycle and vertical distribution of four of the principal species. Bull. Entomol. Res. 40: 149-168.

Mazokhin-Porshnyakov, G.A. 1954. Width of the visible spectrum in insects. Dokl. AN SSSR, 96: 491-493.

_____, 1969. Insect Vision. Plenum Press, N.Y. 306pp.

_____, and T.M. Vishnevskaya, 1965. Berveise der Fahegkeit der Insekten den Kreis: das Dreick und andere einfache Figure zu unterscheiden. Proc. Twelfth Intern. Congr. Entomol. p340.

Meyer, C. and G.F. Bennett, 1976. Observations on the sporogony of Plasmodium circumflexum Kikuth and Plasmodium polare Manwell in New Brunswick. Can. J. Zool. 54: 113-141.

Motte, De la, I. 1972. Ueber die Spektrale Empfindlechkeit des Facettanauges der Marzfliege Bibio marci L. In Vorb.

Newberg, N.D. 1960. Paradoxes in color vision. Priroda 8: 53-59.

Newhouse, V.F., R.W. Chamberlain, J.G. Johnston and W.D. Sudia, 1966. Use of dry ice to increase mosquito catches of the CDC miniature light trap. Mosq. News 26: 30-35.

O'Gower, A.K. 1963. Environmental stimuli and the oviposition behavior of Aedes aegypti, var. queenslandis Theobald (Diptera: Culicidae). Anim. Behav. 11: 189-197.

Peschken, D.P. and A.J. Thorsteinson, 1965. Visual orientation of black flies (Simuliidae: Diptera) to colour, shape and movement of targets. Entomol. Exp. and Appl. 8: 282-288.

Peterson, D.G. and A.W.A. Brown, 1951. Studies of the responses of the female Aedes mosquito. Part III. The response Aedes aegypti (L.) to a warm body and its radiation. Bull. Entomol. Res. 42: 535-541.

Schatz, B. 1971. Ueber die spektrale Empfindlechkeit des Schwebfliegenauges: Elektrophysiologische untersuchungen an Myiatropa florea. Diplomarbeit, Naturwiss. Fak. Univ. Frankfurt.

Schreck, G.E., D.E. Weidhaas, N. Smith and K.H. Posey, 1977. Chemical treatment of wide-mesh net clothing for personal protection against blood-feeding arthropods. Mosq. News 37: 455-462.

Siegal, S. 1956. Non-Parametric Statistics For the Behavioral Sciences. McGraw-Hill Book Co., Inc. N.Y. 312pp.

Sippel, W.L. and A.W.A. Brown, 1953. Studies on the responses of the female Aedes mosquito. Part V. The role of visual factors. Bull. Entomol. Res. 43: 567-574.

Smart, M.R. and A.W.A. Brown, 1956. Studies on the responses of the female Aedes mosquito. Part VII. The effect of skin temperature, hue and moisture on the attractiveness of the human hand. Bull. Entomol. Res. 47: 89-100.

Smith, C.N. and M.M. Cole, 1951. Mosquito repellents for application to clothing. Nat. Malaria Soc. J. 10: 206-212.

Smith, R.F., T.E. Mittler and C.N. Smith, 1973. History of Entomology. Annual Reviews Inc., Calif. 517pp.

Smith, S.M. 1966. Observations on some mechanisms of host-finding and host-selection in the Simuliidae and Tabanidae (Diptera). M.Sc. Thesis, McMaster Univ., Hamilton, Ontario. 144pp.

Snow, W.E. 1955. Feeding activities of some blood-sucking Diptera with reference to vertical distribution in bottomland forest. Ann. Entomol. Soc. Am. 46: 512-521.

Snow, W.F. 1970. The effect of a reduction in expired carbon dioxide on the attractiveness of human subjects to mosquitoes. Bull Entomol. Res. 60: 43-48.

_____, 1971. The spectral sensitivity of Aedes aegypti (L.) at oviposition. Bull. Entomol. Res. 60: 683-696.

_____, 1975. The vertical distribution of flying mosquitoes (Diptera, Culicidae) in West African savanna. Bull. Entomol. Res. 65: 269-277.

Sokal, R.R. and F.J. Rohlf, 1969. Biometrics. W.H. Freeman and Co., San Francisco. 776pp.

Tinbergen, N. 1942. An objectivistic study of the innate behaviour of animals. Bibliotheca Biotheoretica, Leiden, I: 39-98.

Travis, B.V. and F.A. Morton, 1946. Treatment of clothing for protection against mosquitoes. Proc. of the 33rd Ann. Meeting of the New Jersey Extermination Assoc. Atlantic City, N.J. April 3, 4, 5, pp. 65-69.

Tsuneki, K. 1961. Color vision and figure discriminating capacity of the solitary diplopterous wasp, Odynerus fraunfeldi. Saus. Mem. Fac. Liber. Arts Fakui Univ. Ser. 2, 11: 103-160.

Wald, G.J. 1958. Retinal chemistry and physiology of vision. Visual Problems of Color Symposium. Vol 1, No. 8. London.

Weiss, H.B. 1943. Colour perception in insects. J. Econ. Entomol: 36:1-17.

Wenk, P. and G. Schlörer, 1963. Wirtsorientierung und Kopulation bei blutsaugenden Simuliiden (Diptera). Tropenmed. Parasitol. 14: 177-191.

Williams, C.B., R.A. French and M.M. Hosni, 1955. A second experiment on testing the relative efficiency of insect traps. Bull. Entomol. Res. 46: 193-204.

Yahn, T.C. and F. Crescitelli, 1940. Diurnal change in the electrical response of the compound eye. Biol. Bull. 78: 42-52.

Appendix 1

Scientific Names of Species of Culicidae (Diptera) Encountered in the Study.

Aedes abserratus (Felt and Young)*

A. aegypti (Linnaeus)

A. canadensis (Theobald)*

A. cantator (Coquillett)*

A. cinerius (Meigen)*

A. excrucians (Walker)*

A. punctor (Kirby)*

A. sollicitans (Walker)

A. stimulans (Walker)

A. vexans (Meigen)*

Anopheles maculipennis (Meigen)

An. taeniorhynchus (Wiedemann)

An. walkeri (Theobald)*

Culiseta morsitans (Theobald)*

Mansonia perturbans (Walker)*

*Species Collected in this study.

Appendix 2

Summary of Chi-squared Tests of Paired Filter Experiments Study 4, Part B, Trials 1,2 and 3 (Tables 18, 19 and 20).

Filter Pairs	Trials		
	1	2	3
47B X 61	$p<.001$	$p<.001$	$p<.001$
47B X 92	$p<.001$	$p<.001$	$p<.001$
47B X 18A	$p<.001$	$p<.001$	$p<.001$
47B X 88A	$p<.001$	$p<.001$	$p<.001$
61 X 92	$p<.001$	$p<.001$	$p<.001$
61 X 18A	$p<.001$	$p<.001$	$p<.001$
61 X 88A	$p<.001$	$p<.001$	$p<.001$
92 X 18A	$p<.005$	$p<.001$	$p<.005$
92 X 88A	$p<.001$	$p<.001$	$p<.001$
18A X 88A	$p<.001$	$p<.001$	$p<.001$